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Ichnology of Carboniferous and Jurassic Tetrapods and Insects

Patrick R. Gonsoulin-Getty
University of Connecticut - Storrs, patrick.getty@uconn.edu

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Patrick Ryan Gonsoulin-Getty, PhD

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Ichnology is the study of trace fossils such as tracks, trails, and burrows. Such fossils are important because they provide direct evidence of animal behavior and because, as sedimentary structures, they are often preserved in environments inimical to the preservation of body fossils. This study looks at why skeletal fossils are rare in southern New England and uses ichnology to evaluate the behaviors of its Carboniferous and Jurassic inhabitants.

The first chapter addresses taphonomic processes that preserved dinosaur bones from Middletown, Connecticut as molds rather than bone. Observations suggest that the animal died and decomposed above ground, where its skeleton disarticulated and was transported fluvially. The bones later were buried and dissolved underground due to acidic groundwater. Their preservation as molds provides a rare glimpse at the taphonomic processes limiting body fossil preservation in the Hartford Basin.

The second chapter presents a comprehensive remapping of Dinosaur Footprint Reservation in Holyoke, Massachusetts, to test whether gregarious behavior existed in local dinosaur communities after the Triassic extinction. The orientations of the tracks were compared to the direction of the paleoshoreline, as indicated by oscillation ripples. Analysis indicates that large carnivores and small herbivores paralleled the shore, whereas small carnivores preferred to walk perpendicular to it. These data support the

idea that dinosaur-dominated ecosystems in the early Jurassic were fish-based rather than based on terrestrial herbivores.

The third chapter uses experimental ichnology to determine the maker of unusual Carboniferous trackways. Modern jumping bristletails and silverfish were used as analogues for the primitive insects that made the traces, and the experiments show that slightly different orientations of the tail appendages in life can explain the differences in fossil trackway morphology.

Finally, the fourth chapter presents a new reconstruction of continental occurrences of the well-known fossil fly burrow called *Treptichnus* based on well-preserved specimens from the Jurassic of Massachusetts. Thin sections indicate that the burrows, which were probably made by insect larvae, were largely horizontal, in contrast to previous reconstructions.

Ichnology of Carboniferous and Jurassic Tetrapods and Insects

Patrick Ryan Gonsoulin-Getty

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Presented by

Patrick Ryan Gonsoulin-Getty, B.S., M.S.

Major Advisor _____
Andrew Bush

Associate Advisor _____
Pieter Visscher

Associate Advisor _____
David Wagner

University of Connecticut

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PREFACE

Ichnology of Carboniferous and Jurassic Tetrapods and Insects

There are two large sedimentary basin complexes in southern New England, each of different ages. In the east, stretching northeast from Narragansett Bay in Rhode Island to the Atlantic shores of Marshfield, Massachusetts, is the Paleozoic Narragansett Basin and its associated basins. Farther west, approximately following the Connecticut River Valley from New Haven, Connecticut to Northfield, Massachusetts is the Mesozoic Hartford Basin and its associated, smaller basins. Each of these basin complexes is filled with fossils of their former inhabitants. Most of the fossils of the animals, however, consist of traces produced by the living animals, rather than their skeletons.

Mesozoic trace fossils of the Hartford Basin have been known since 1802, when a young boy in South Hadley, Massachusetts plowed them up in his field. Edward Hitchcock, a professor at Amherst College, studied the Mesozoic traces in great detail from the 1830's through the 1860's and is now credited with developing the science of ichnology as its own discipline. Since the days of Hitchcock, other researchers have continued to study these traces to determine what made them and to understand early Mesozoic ecosystems. Despite the long history of work on these fossils, there is still plenty of research to be done. Here I present the results of my work on Early Jurassic dinosaur tracks to determine how these animals behaved in relationship to a large lake that they lived next to, and my work on the traces of early flies that lived and burrowed under the feet of the dinosaurs.

In contrast to the Mesozoic trace fossils from western New England, the

Carboniferous ones in the southeast are much less well known and studied. There are many reasons why these fossils remained understudied until recently, not the least of which is the fact that the rocks in which they are preserved were tectonically deformed and mildly metamorphosed during the building of Pangea in the Permian Period. The deformation and metamorphism apparently destroyed most, if not all, trace fossils in the southern part of the basin. Luckily, in the north of the basin, where deformation and metamorphic grade are less, traces can still be seen, although they are clearly warped. Their deformation aside, these fossils represent an important record of life during an important interval in Earth's history as the first amniotes evolved. Paleontologists have long wondered what sorts of animals lived in New England in the Carboniferous, which is situated between the great Carboniferous fossil-bearing rocks of the Canadian Maritime Provinces and those of the southern Appalachians, and with the recent exposure of many of these rocks and their analysis, now they can know. In the third chapter of this dissertation, I present a study I conduced on the fossilized body imprints and trackways of the early insects that lived here at the time.

Sand pseudomorphs of dinosaur bones: implications for (non-) preservation of tetrapod skeletal material in the Hartford Basin, USA

ABSTRACT

Early Jurassic vertebrate tracks are common in the Hartford Basin (Newark Supergroup) of Connecticut and Massachusetts, USA, but skeletal material is rare. Among the few examples is a set of several bones preserved as natural casts on the base of a slab of arkosic sandstone that probably derived from the Portland Formation of Middletown, Connecticut. This mode of preservation is otherwise unknown in the Hartford Basin, and examination of this specimen suggests a complex taphonomic history. After disarticulation, the bones were hydrodynamically sorted, oriented, and emplaced in a muddy substrate. Longitudinal cracks, missing flakes, breakage, rounding, and invertebrate boring indicate significant alteration prior to burial. Furthermore, the boring represents the first record of osteophagy in the Hartford Basin. Details of the cast preservation suggest that the original bone material was dissolved in the subsurface prior to lithification of the overlying sand bed. The depauperate skeletal fossil record of the Hartford Basin is attributable to dissolution due to acidic and/or oxidative soil and sediment conditions; these natural casts offer a unique view of the actions of this taphonomic process.

1. Introduction

Exceptionally preserved fossils such as feathered dinosaurs and Burgess Shale-type fossils attract considerable interest because of the unique information they provide about evolution and paleoecology. However, there is also increasing interest in the opposite

phenomenon: the non-preservation fossils. Organic and mineralized tissues are preserved only under specific conditions, and when these conditions are not met, biological remains can be lost to physical, chemical, or biological destruction (e.g., Koch and Sohl, 1983; Retallack, 1984; Cherns and Wright, 2000; Seilacher et al., 2001; James et al., 2005). If exceptionally preserved fossils provide unique views of ancient life, episodes of non-preservation represent blind spots that can limit or bias our understanding of the history of life (Sessa, 2009; Hendy, 2009). Thankfully, sediments can provide some informational redundancy in the fossil record (Bush and Bambach, 2004)—trace fossils record the activities of organisms that may not be preserved, and molds, casts, and impressions can record morphology even when the original body fossils are destroyed (McAlester, 1962).

The Early Jurassic strata of the Hartford and Deerfield Basins of Connecticut and Massachusetts provide an interesting case study in the non-preservation of body fossils. Tetrapod skeletons are quite rare, but their footprints are plentiful and have attracted attention since the seminal works of Hitchcock (1848, 1858, 1865) and Deane (1865). The identities of the tracemakers are known, at least at a high taxonomic level, with examples of theropods, prosauropods, ornithischians, and crocodylomorphs represented (Olsen and Padian, 1986; Olsen et al., 1998; Olsen and Rainforth, 2003; Rainforth, 2003). Thus, we know what should be found in the body fossil record, and, indeed, the trace fossil record is consistent with the few skeletons that have been found (see section 5, below).

Given the paucity of the skeletal record, there has been a sense that the sediments and soils of the Hartford Basin must have been chemically inhospitable to the preservation of bone (e.g., McDonald, 1992, 1996). Here, we analyze the taphonomy of one of the few skeletons

recovered from the Hartford Basin and offer support for the hypothesis that bone dissolution occurred in the Early Jurassic of New England.

2. Materials and History of Study

Rogers (1864) discovered one of the few examples of skeletal material from the Hartford Basin—a natural cast of dinosaur bones preserved on the base of a slab of arkosic sandstone (Fig. 1). He found the specimen at a construction site in Newport, Rhode Island, and traced its origin to Middlebury, Connecticut. However, the bedrock of Middlebury is Cambrian-aged schist and gneiss (Rodgers, 1985), and Colbert and Baird (1958) proposed that Middlebury was a typographical error for Middletown, where large sandstone quarries operated during the 19th century. Other workers have followed suit, and consider the source of the bones to be the Lower Jurassic Portland Formation of Middletown or a nearby town (e.g., Olsen, 1988; McDonald, 1992; Galton and Farlow, 2003).

Rogers acquired the slab for the Boston Society of Natural History (BSNH), and a replica was sent to the British Association for the Advancement of Science. Members of both societies considered the specimen an important find (Rogers, 1864, 1865). British zoologists noted the bones' combined reptilian and avian characteristics, which they considered evidence that the Hartford Basin footprints were produced by a reptile or "semi-reptile" trackmaker. In contrast, Hitchcock (1848, 1858, 1865) argued that birds produced many of the footprints.

Despite the early importance given to the specimen, it was later neglected, probably due to the deaths of Edward Hitchcock and Henry Rogers (Colbert and Baird 1958) and the decline and eventual closure of the BSNH (Johnson, 2004). The specimen was put into storage, along with the remainder of the BSNH collection, around 1946 (Johnson 2004), and then relocated

and described by Colbert and Baird (1958). These authors noted that the bones themselves were not preserved; rather, the fossils were natural casts that formed when sand filled the impressions left by the bones in a muddy substrate. They identified the bone casts as the right pubis, tibia, and several ribs of *Coelophysis*, a small theropod known from New Mexico (also see Colbert 1964). Later workers (e.g., Olsen, 1980, Padian, 1986, Rowe and Gauthier, 1990, Tykoski and Rowe, 2004) have noted that this identification was based only on plesiomorphic characteristics and that the bones cannot be diagnosed below the suborder Theropoda. Also, Olsen (1980) observed that the Hartford Basin material is approximately 15 million years younger than *Coelophysis*, so it likely represents another taxon. Given the fragmentary nature of the specimen, most recent workers have kept it in open nomenclature (Olsen, 1980; Padian, 1986; Rowe and Gauthier, 1990; Tykoski and Rowe, 2004), which we follow here. Although it would be useful to know how to classify this specimen, it is not necessary for the present taphonomic study.

The specimen is currently on display at the Boston Museum of Science (MOS 2001.248). Replicas made prior to this study are housed at the American Museum of Natural History (FR 7636), Amherst College Museum of Natural History (ACM 11793c), Museum of Comparative Zoology (MCZ 2768), and Yale Peabody Museum (YPM 3912). Whether the replica presented to the British Association for the Advancement of Science still exists is unknown. For this study, a silicone peel of the original specimen was made using oomoo® 30 silicone rubber. This peel replicates the muddy substrate into which the bones were originally impressed. Replicas of the specimen were then made from the peel using hydrocal® high-strength gypsum cement and Smooth-Cast 300® liquid plastic.

3. Geological Context

The Hartford Basin is an asymmetrical half graben that formed during the Late Triassic through Early Jurassic, during the breakup of Pangaea. The Early Jurassic Portland Formation is the uppermost stratigraphic unit in the basin and is divided into a lower, primarily lacustrine unit, and an upper, primarily fluvial unit (Olsen et al., 2005). This facies change resulted from changes in crustal extension rates (Olsen, 1997); during the early phases of Portland deposition, crustal extension rates were high, sediment accumulation could not keep up with accommodation, and lacustrine conditions predominated. As crustal extension slowed in the Pleinsbachian, sediment filled the basin to its rim, and fluvial conditions were established. Whereas dinosaur tracks from the Hartford Basin are known from a variety of environments, most of the depauperate skeletal record is derived from the fluvial deposits of the upper Portland and underlying New Haven Formations (Olsen, 1988).

The upper fluvial facies of the Portland Formation is exposed in and near Middletown, and the limited sedimentological evidence from MOS 2001.248 is consistent with an origin in these strata. The lower portion of the slab is planar laminated, fine- to coarse-grained, arkosic sandstone above which are three graded bedding sequences (Fig. 2). The underlying bed was composed of mud, as indicated by the thin shaly layers adhering to the underside of the slab near the bone casts. A mud lamina is exposed on one side of the slab as well.

The muddy bed on which the bones came to rest was scoured before it was buried in the overlying sand, as indicated by small flutes (boxed in Fig. 1), which can be used to infer a flow direction from lower left to upper right in Fig. 1. Elongate (maximum length 6 cm), slightly sinuous ridges of sediment with cuspate crests (labeled srr in Fig. 1) are here interpreted as scour remnant ridges (Allen, 1965; 1982) and provide additional evidence for bed scouring. In

profile, some of these ridges are highly asymmetric, with a steep face in the inferred up-current direction and a tapering face in the inferred down-current direction. Finally, the bones themselves may have served as an obstacle around which scouring occurred. The bones are arranged in a v-shape, the apex of which is oriented in the inferred upstream direction (see section 4.2, below). Immediately up-current from the bones is a broad shallow depression that likely resulted from turbulent flow around the bones. Several ripples (labeled ri in Fig. 1) are cast on the base of the sandstone near the pubis, and they indicate a flow direction perpendicular to that inferred from other structures. However, these appear to represent the casting of a slightly lower depositional surface than the other structures, and may have been exhumed during the scouring of the muddy layer.

4. Taphonomy

Colbert and Baird's (1958) study of this specimen was not focused on taphonomy, but they proposed a simple sequence of events to explain the preservation of the bones as casts: the bones were transported by water and came to rest on a muddy substrate, which then hardened enough to remain intact when flood waters washed the bones away. The molds left by the bones were filled by sand carried by the floodwaters.

A closer examination of the specimen reveals additional taphonomic details unaddressed by Colbert and Baird (1958). Moreover, further examination suggests that the bones were not removed from the muddy substrate by currents and then cast by sand; instead, the bones were probably dissolved *in situ* after burial. This mode of preservation has obvious implications for the paucity of preserved skeletal material from the Connecticut Valley. Below, we discuss the taphonomic processes that affected these bones in sequence.

4.1. Hydrodynamic Sorting

Colbert and Baird (1958) identified the bones as a pubis, tibia, and several ribs of a small theropod dinosaur (whether the bones represent a single or multiple individuals is unclear). In addition, a fragment that these authors did not identify may represent a partial cervical vertebra (v? in Fig. 1). Assuming that these identifications are correct, the arm bones, many of the leg bones, most of the vertebrae, the skull, and the sacrum of the animal(s) are missing. However, it is impossible to know if some or all of these bones were deposited nearby because the specimen was moved from its original geological context prior to collection.

The fragmentary nature of the skeleton and the types of bones present can be explained by the sorting that disarticulated skeletons undergo in flowing water. The transport potential of a bone is related to its shape and density: in general, small, light bones are easy to transport, whereas large, dense bones are more difficult to transport (Voorhies, 1969; Behrensmeyer, 1975; Boaz and Behrensmeyer, 1976; Gifford and Behrensmeyer, 1977; Aslan and Behrensmeyer, 1996; Blob, 1997; Trapani, 1998). The bones preserved on MOS 2001.248, with the exception of the possible vertebra, are all relatively similar in size and shape—they are all long bones— supporting an interpretation of hydrodynamic sorting. The most easily transported bones (e.g., vertebrae and small bones from the hands and feet) are generally not present, and were presumably transported further by currents. The one possible vertebra is located downstream from the pubis and ribs, and was probably deposited in the lee of these bones due to decreased current velocity in that region. Skulls are generally among the least transportable of bones, and the skull (or skulls) associated with these bones may have been transported a shorter distance.

Although flume experiments have shown that ribs are transported more easily than limb bones, Aslan and Behrensmeyer (1996) reported observing accumulations of ribs and long bones along the East Fork River in Wyoming. These authors proposed that under natural conditions, rib shafts get buried quickly, slowing their movement downstream. Considering that ribs and long bones in modern environments can accumulate as a single deposit, it seems reasonable to conclude that the ribs and long bones on MOS 2001.248 resulted from a similar pattern of hydrodynamic dispersal.

4.2. Bone Orientation

As noted, the orientation of scouring features indicates water flow from the lower left to the upper right of Figure 1, as indicated by the arrowhead. Most of the bones, with the exception of one of the ribs (r3 in Fig. 1), are oriented with their long axes approximately parallel to the inferred flow direction. Unlike the other bones, rib 3 is oriented perpendicular to the current. The orientations of the bones are consistent with observations that elongate objects tend to align either parallel or perpendicular to a current (Voorhies, 1969; MacDonald and Jefferson, 1985). Furthermore, objects with ends of different sizes tend to align with the wider end oriented downstream (Voorhies, 1969; Boaz and Behrensmeyer, 1976; MacDonald and Jefferson, 1985), as is seen with the pubis on MOS 2001.248 (Fig. 1).

The v-shaped arrangement of long bones suggests that they might have been ensnared on an obstacle. Sticks and other elongate objects produce similar v-shaped structures as they are carried in streams and get caught on obstacles (Figure 3; sticks are of course not exactly analogous to bones, but as elongate objects, their behavior is similar in this respect). As one end of the object hits the obstacle, the free end pivots around the obstacle until it points

downstream. As objects catch on opposite sides of the obstacle, the characteristic v-shape develops. In this way, the v-shaped arrangement of the bones further supports the inferred flow direction.

4.3. Bone Weathering and Bioerosion

The bones on MOS 2001.248 were significantly weathered; all exhibit cracking and/or flaking (Fig. 4). The proximal articular surfaces of the pubis are rounded, likely as a result of abrasion during transport, and the distal portion of the pubis is broken, jagged, and bears longitudinal cracks (Fig. 4a, labeled lc). The tibia is broken into proximal and distal sections, and a large flake measuring 3.4 by 0.9 cm has fallen away from the proximal end (Fig. 4a, labeled f). The distal end of the tibia is cracked longitudinally, and bone fragments have flaked off there as well (Fig. 4b, labeled f). The rates at which bones weather vary among taxa and environments (Toots, 1965; Behrensmeyer, 1978; Andrews, 1995; Andrews and Armour-Chelu, 1998), but in any case, these highly weathered bones were exposed for a considerable time after death. The inferred duration of exposure is consistent with evidence cited above for disarticulation, transport, and sorting.

In addition to the cracks and flakes, a long groove measuring 2.6-5.1 mm deep and 2.3-8.5 mm wide crosses the pubis (Fig. 5), dividing the bone into a small proximal articular region and a long shaft. Colbert and Baird (1958) interpreted the groove as a fracture in the bone around which the shaft of the pubis had rotated, such that it lay in the mud obliquely. However, the contours of both halves of the pubis are still aligned, suggesting that parts of the

pubis did not move relative to each other. In addition, the detailed morphology of the groove suggests that it is not a fracture. It meanders across the bone and has, in places, smaller, lobes projecting away from it. The walls of the groove are variably sloped and in some places nearly vertical; on one side, bone overhangs the groove. In some places the bottom of the groove is smooth and rounded, whereas in others the bottom is variable and irregular. There are small (sub-millimeteric) striae (Fig. 5c) that vary in direction in parts of the groove, many paralleling the wall of the channel.

The groove's sinuous nature, lobate projections, fine-scale striae, and overhanging edges are consistent with the furrows generated by osteophageous insects (Britt et al., 2008). The lobate projections likely represent small branches off the main furrow produced by probing activity, and the fine-scale striae may represent mandibular scratch marks. Numerous insects are known to feed on bone (Smith, 1986); however, we have not attempted to identify the tracemaker specifically given that the original bone and boring are not present for detailed examination. Nonetheless, this boring represents the first evidence for the activities of bone-eating insects in the Hartford Basin, which is not surprising given that skeletal material is rare and that many of the preserved skeletons were probably rapidly buried (see section 5).

4.4. Cast Formation

As noted previously, Colbert and Baird (1958) proposed that the bones were preserved as casts when floodwaters ripped them out of the mud and deposited sand in their place. Conceivably, the bones could have been removed by other physical mechanisms as well: they could have been lifted vertically from the substrate by a scavenging animal or by floatation, leaving hollow molds that were later infilled with sand.

There are several difficulties with the hypothesis that currents removed the bones. There are no prod or drag marks, which might have been produced as the bones were carried away as bed load. Furthermore, the downstream ends of the molds are not deformed, as would be expected if the bones had been pivoted out of the mold as they were ripped free of the bed. Additionally, it seems highly unlikely that currents strong enough to erode the bones and deposit the planar-bedded sandstone would leave the molds completely undamaged. The molds exhibit fine-scale details of the bones, including all of the weathering features discussed above. Although it is possible that the mud may have hardened before the sand filled the molds, or that a microbial mat stabilized them, there is no evidence to support either scenario. The slab preserves no sedimentary structures that would indicate subaerial exposure (and thus, potentially, hardening), such as raindrop impressions or desiccation cracks. Neither is there conclusive evidence of microbially-produced sedimentary structures (e.g., Hagadorn and Bottjer, 1997; Schieber, 1998; Noffke et al., 2001), although had a microbial mat been present, it is possible that the mat could have stabilized the bones as well, preventing them from being dislodged by the current.

Most importantly, the bones were embedded deeply in the muddy substrate (up to 7 mm), and cross-sections of replicas demonstrate that the mud, in places, wrapped up and slightly over the tops of the bones (Fig. 6), which would not be the case if the bones had been physically uprooted from the substrate. It is theoretically possible that the sediment rims appear to drape over the tops of the bones due to slumping after the removal of the bones, but it is not clear why the slumping always occurred towards the bones and why the rims were not damaged in what would have been an intense current. In addition, sediment slumping would require that the mud was soft when the bones were removed, making it even more difficult to

explain how the rims were not damaged in a high-energy, sand-laden current. Indeed, these rims—the boundaries between the bones and the surrounding sediment—are sharp, high-relief structures, and were not abraded (Figs. 4 and 6).

Based on this evidence, we argue that the bones were buried in the high-energy event represented by the fine- to coarse-grained arkosic sandstone and that they were later dissolved by groundwater. The overlying sand filled in the resulting cavities. Although this scenario cannot be proven beyond doubt, it alone explains the high level of detail preserved in the casts, and the sediment rims that slightly overlapped the bones. Surficial dissolution is possible but less likely; it can explain the rims overlapping the bones, but not the high preservational quality of the rims. It is worth noting that similar arguments have been made for invertebrate trace fossils such as *Cruziana*—structures produced infaunally are better preserved than similar traces that are scoured out and then cast (Goldring, 1985).

4.5. Processes of Bone Dissolution

Bone dissolution is probably a common process in the geological record, at least under certain conditions. For example, Seilacher et al. (2001) described sideritic coprolites or "cololites" that were preserved in strata with no skeletal material, which they attributed to dissolution. Similarly, Retallack (1984, 1988) observed that in the Badlands of South Dakota, bones occurred in calcareous paleosols, but not in non-calcareous paleosols, which he attributed to dissolution under acidic conditions.

Bone dissolution is dependent on pH and oxidation-reduction potential (Rapp and Hill 2006)—the more acidic or oxidative an environment, the faster dissolution will take place. Pike et al. (2001) noted that the solubility of hydroxyapatite increases tenfold for every

decrease of 1 in pH. The concentration of Ca^{+} and PO_4^{3-} ions in the groundwater or soil and the rate of groundwater recharge also affect dissolution rate (White and Hannus, 1983; Hedges and Millard, 1995; Pike et al., 2001; Hedges, 2002). Soils high in Ca^{+} and PO_4^{3-} result in slow dissolution because the substrate is already near saturation levels in respect to these ions, which are dissolution products. In contrast, dissolution may be increased in more acidic soils rich in iron and aluminum, as PO_4^{3-} ions combine with Fe^{3+} and Al^{3+} to precipitate iron- and aluminum-bearing phosphates. Continuously flowing water also promotes bone dissolution by carrying away dissolved ions, preventing localized saturation with dissolution by-products. Dissolution also may be enhanced by bone porosity, which increases with protein loss and microbial decay.

The sediment and bones in MOS 2001.248 have some of the characteristics described above that promote dissolution. For example, both iron and aluminum would have been available to combine with phosphate ions: iron from the dissolution of biotite, hornblende, and augite (Hubert and Reed, 1978; Hubert et al., 1992; Hubert et al., 2001), and aluminum leached from Lower Paleozoic gneisses and schists and transported by rivers and groundwater (Hubert et al., 2001). Additionally, water would have percolated readily through the overlying sand, whereas the mud underlying the bones would have served as an aquitard, forcing groundwater to flow through the bones, which were at the mud-sand interface. The weathered bones had a higher surface to volume ratio than fresh bone, making them more susceptible to dissolution.

Although it is impossible to determine how fast the dinosaur bones dissolved, it must have occurred before the overlying sand was lithified. Hubert et al. (1992) suggested that sandstones of the Hartford Basin were cemented at relatively shallow depths (< 1km). However, considering that modern bones found in some acidic soils are severely weathered

within 20 years of burial, and are completely dissolved within 700 years (Watson, 1967), it is possible that dissolution was rapidly completed very near the surface.

5. Preservation of Other Connecticut Valley Skeletons

In addition to MOS 2001.248, Hartford Basin theropods are represented by an isolated tooth (McDonald, 1992) and by *Podokesaurus holyokensis*, which was found in a glacial erratic (Talbot, 1911). *P. holyokensis* is fairly complete, although the tail disarticulated as a unit from the body. The skull and cervical vertebrae are missing, but it is unknown if they were part of the fossil before glacial transport. In any case, the relative completeness of the animal indicates that it was buried quite rapidly (Holz and Barberena, 1994).

Prosauropod dinosaurs are represented by seven specimens from the Hartford Basin (Smith, 1820, Hitchcock, 1855; Marsh, 1889; Galton, 1976). Two specimens were found during blasting for wells, and as such are fragmentary. However, both are composed of articulated forelimbs (Galton, 1976, figs. 7 and 32), suggesting burial before complete disarticulation. A quarry in Manchester, Connecticut, produced three articulated and well-preserved skeletons, as well as two poorly preserved skeletons. One specimen (YPM 1883) is nearly complete and includes an articulated skull (Galton, 1976, figs. 11-13).

Various other reptiles have been found in the Hartford Basin. The crocodylomorph *Stegomosuchus longipes* (Emmerson and Loomis, 1904) retains its dermal armor, indicating rapid burial before disarticulation. *Erpetosuchus*, a crocodile-like archosaur, is known from a partial skull, poorly preserved vertebrae, and bone fragments (Olsen et al., 2000). Phytosaurs are represented by a partial scapula (Marsh, 1893; Lull, 1953), and the aetosaur *Stegomus arcuatus* is represented by molds of parts of the dermal armor (Marsh, 1896; Lucas et al.,

1998). *Hypsognathus fenneri*, a small, lizard-like anapsid reptile, is known from a partial skull (Sues and Baird, 1993), as well as a more complete specimen (Sues et al., 2000), again indicating rapid burial before disarticulation. The latter specimen is preserved as a hollow mold formed when the bones dissolved after the sediment lithified.

As can be seen from the above survey, none of the other vertebrate skeletal remains are preserved as natural casts, and many specimens are at least partly articulated. Thus, the preservation of the bones on MOS 2001.248 as weathered, disarticulated, hydrodynamically sorted natural casts is unique in the tetrapod record of the Hartford and Deerfield Basins. Some of the other specimens are molds, indicating that the skeletal material dissolved away, but dissolution occurred after lithification. Given that the sediments of the Hartford and Deerfield Basins were generally inimical to the preservation of bone, it would be worthwhile to examine the local environmental and diagenetic conditions that permitted the preservation of original skeletal material in these other specimens.

6. Conclusions

MOS 2001.248 is a slab of arkosic sandstone whose base preserves the natural casts of bones of one or more small theropod dinosaurs. The bones were transported by flowing water after the death and disarticulation of the animal(s), and the deposit of long bones resulted from hydrodynamic sorting. When the bones were deposited, the current was still strong enough to orient the bones, four of which were arranged into a "V" pointing upstream, and one of which was oriented perpendicular to the flow. The bones exhibit longitudinal cracks, missing flakes, an insect boring, and broken ends, which indicate significant weathering before deposition. The insect boring represents the first example of osteophagy recorded from the Hartford Basin.

The natural casts could have formed via several preservational pathways, including the following: 1) physical removal of the bones at the surface followed by infilling of the molds, or 2) chemical dissolution of the bones, either at the surface or underground, prior to lithification. We argue that the bones dissolved after burial because scouring, which has affected the surrounding sediment surface, did not destroy or abrade the bone molds. Furthermore, the edges of the molds overlapped some of the bones, suggesting that the bones were not physically removed. Dissolution of the bones would have resulted from acidic and/or oxidative groundwater, and the porous, overlying sand would have permitted water flow past the bones, increasing the dissolution rate. In addition, iron and aluminum ions may have increased the rate of dissolution by lowering phosphate concentrations.

Dinosaurs and other tetrapods were abundant in Connecticut and Massachusetts during the Early Jurassic, as evidenced by their abundant trace fossil record. The sediments were generally inimical to the preservation of bone, however, and the bone casts discussed here provide a unique window into the activity of bone dissolution as a taphonomic process. Given the generally poor preservation potential of bone in this region, it would be worthwhile to examine the unique paleoenvironmental and taphonomic circumstances that result in its rare preservation.

Figure 1. MOS 2001.248, a slab of arkosic sandstone that probably derives from the Early Jurassic Portland Formation of Middletown, Connecticut. The bones of a small dinosaur are preserved as natural casts on the lower surface of the slab, shown here. The white box encloses a small flute, and the arrowhead next to it indicates the approximate direction of current flow. Abbreviations: dp, distal pubis; pp, proximal pubis; pt, proximal tibia; dt, distal tibia, r1-r3, ribs 1-3 respectively; v?, possible vertebra; ri, ripples; srr, scour remnant ridges; u, unidentified structure between pubis and tibia.

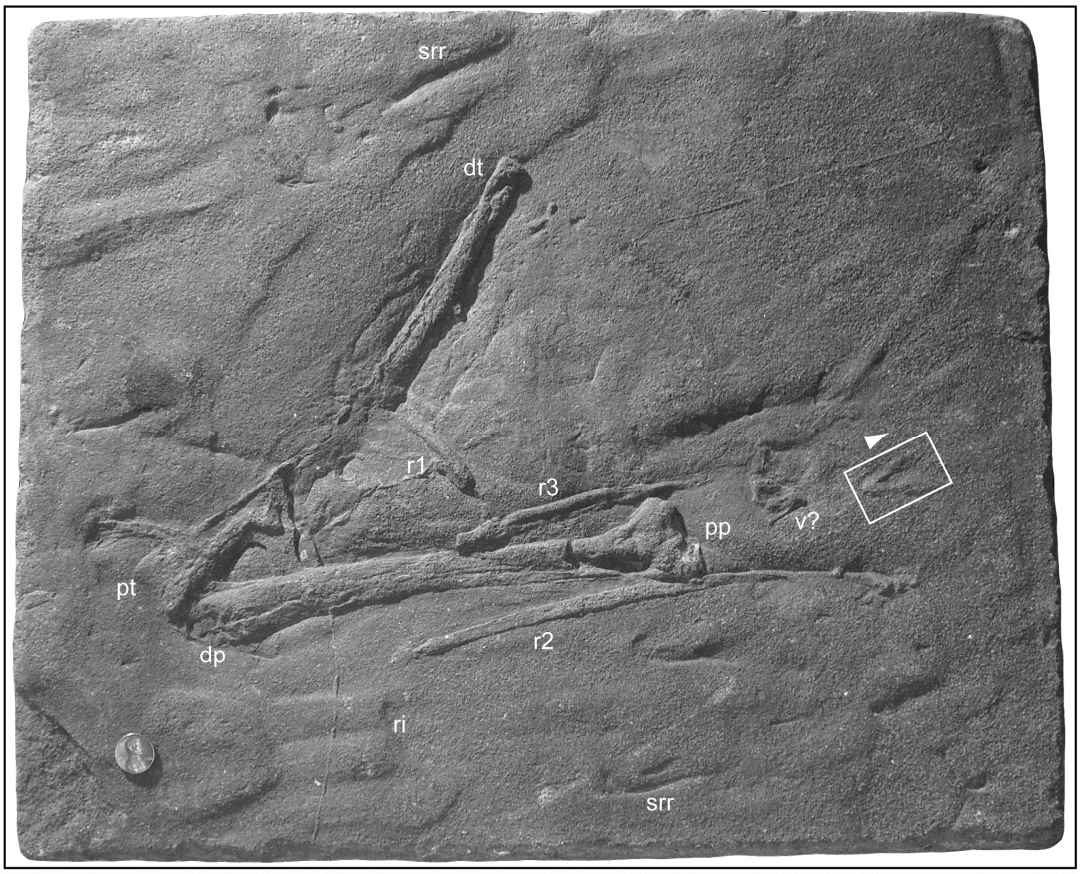

srr
dt
r1
r3
pp
v?
pt
dp
r2
ri
srr

Figure 2. V-shaped arrangements of sticks observed in a stream. Cluster A occurred naturally where sticks became caught on an obstruction, whereas cluster B was generated when sticks were placed in a current upstream of an obstacle to observe how the v-shaped pattern formed. Although sticks are not exactly analogous to bones, they are elongate objects and their behavior is similar in this respect. Stream flow is from left to right. Field of view at top of photograph is ~ 1 m. Compare to the arrangement of the fossil bones in Figure 1.

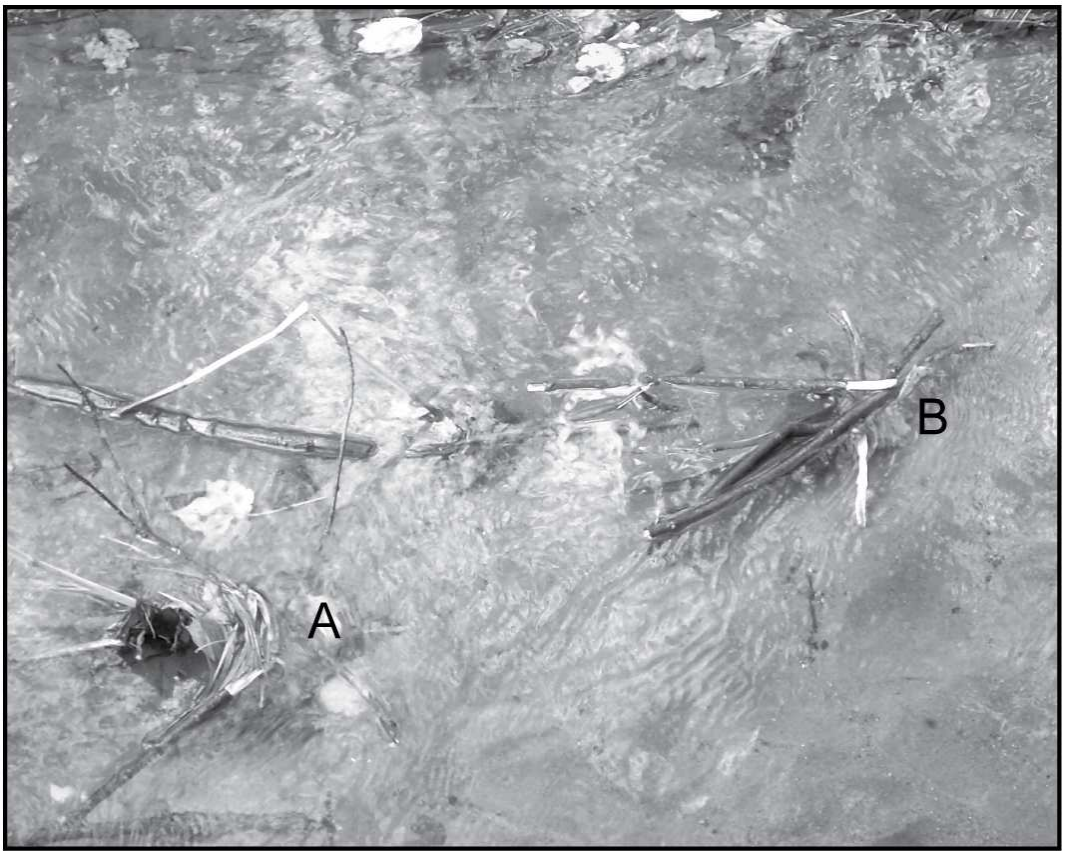

A
B

Figure 3. Damage to the bones. (A) Close-up of distal end of pubis, proximal end of tibia, and portions of the ribs. (B) Close-up of distal tibia. Abbreviations: bo, boring; g, gouge; lc, longitudinal crack; u, unidentified structure between pubis and tibia. Scale indicated by a 1.9 cm diameter coin.

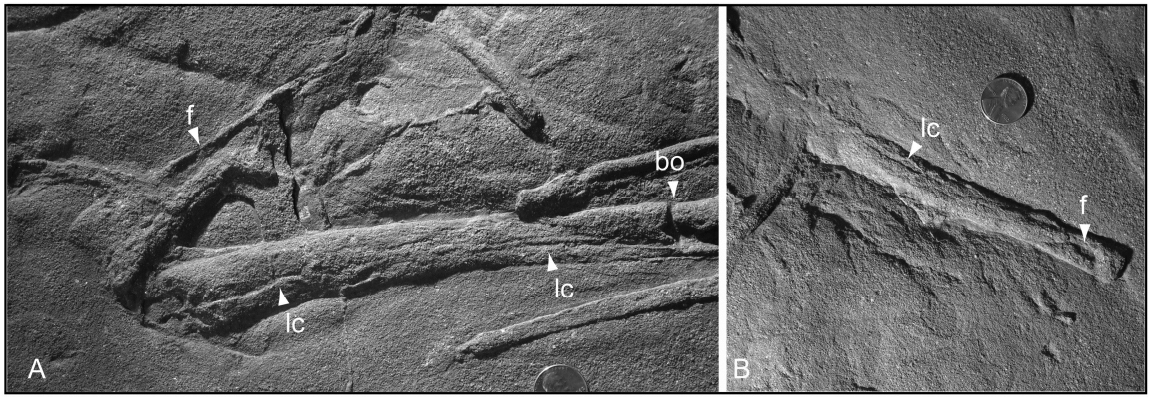

f
bo
lc
lc
A
lc
f
B

Figure 4. Probable invertebrate damage on the underside of the pubis. (A) Replica of the proximal pubis showing sinuous boring. Note the slight disruption to the sediment (labeled d) where the boring contacts the substrate next to the bone. This suggests that the boring was produced after the bone was embedded in the mud (B) Rubber mold of the proximal pubis showing impression of the boring. Arrowheads point to lobate projections (labeled lp) that may represent probing activity of the borer. (C) Close-up of the boxed area in panel (B). Arrowheads point to millimeter scale striae that only occur within the boring, and which may have been produced by the borer. Scale is 1 cm in all images.

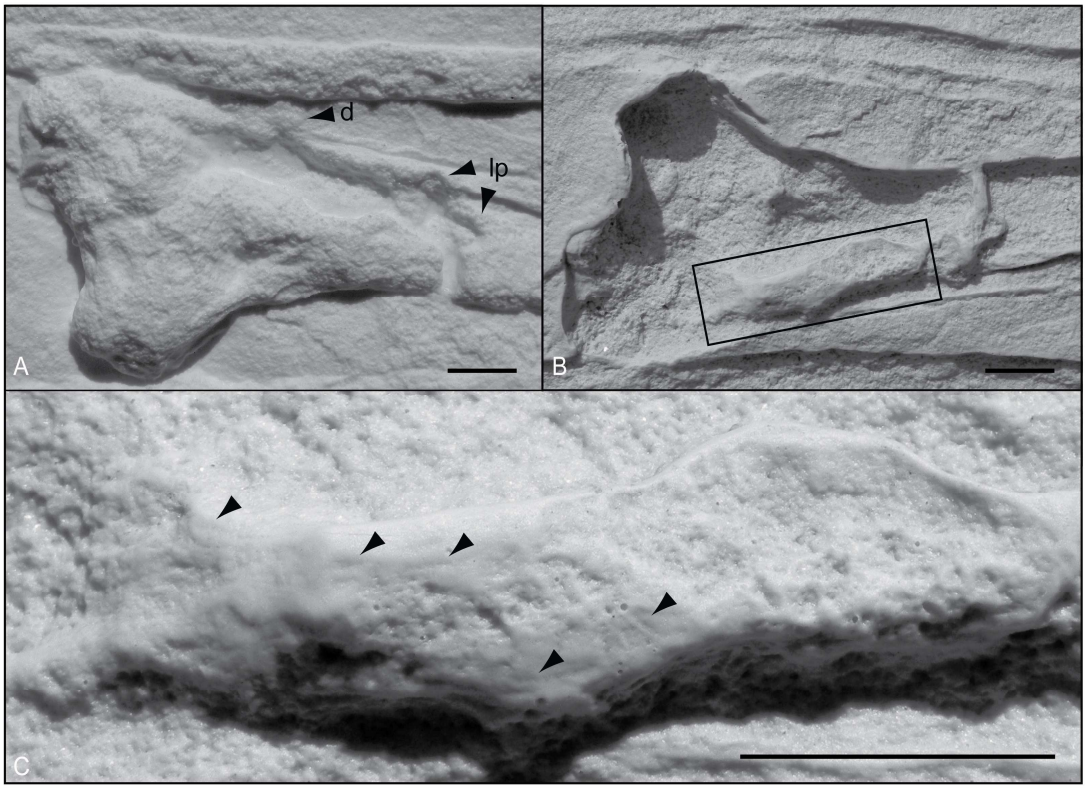
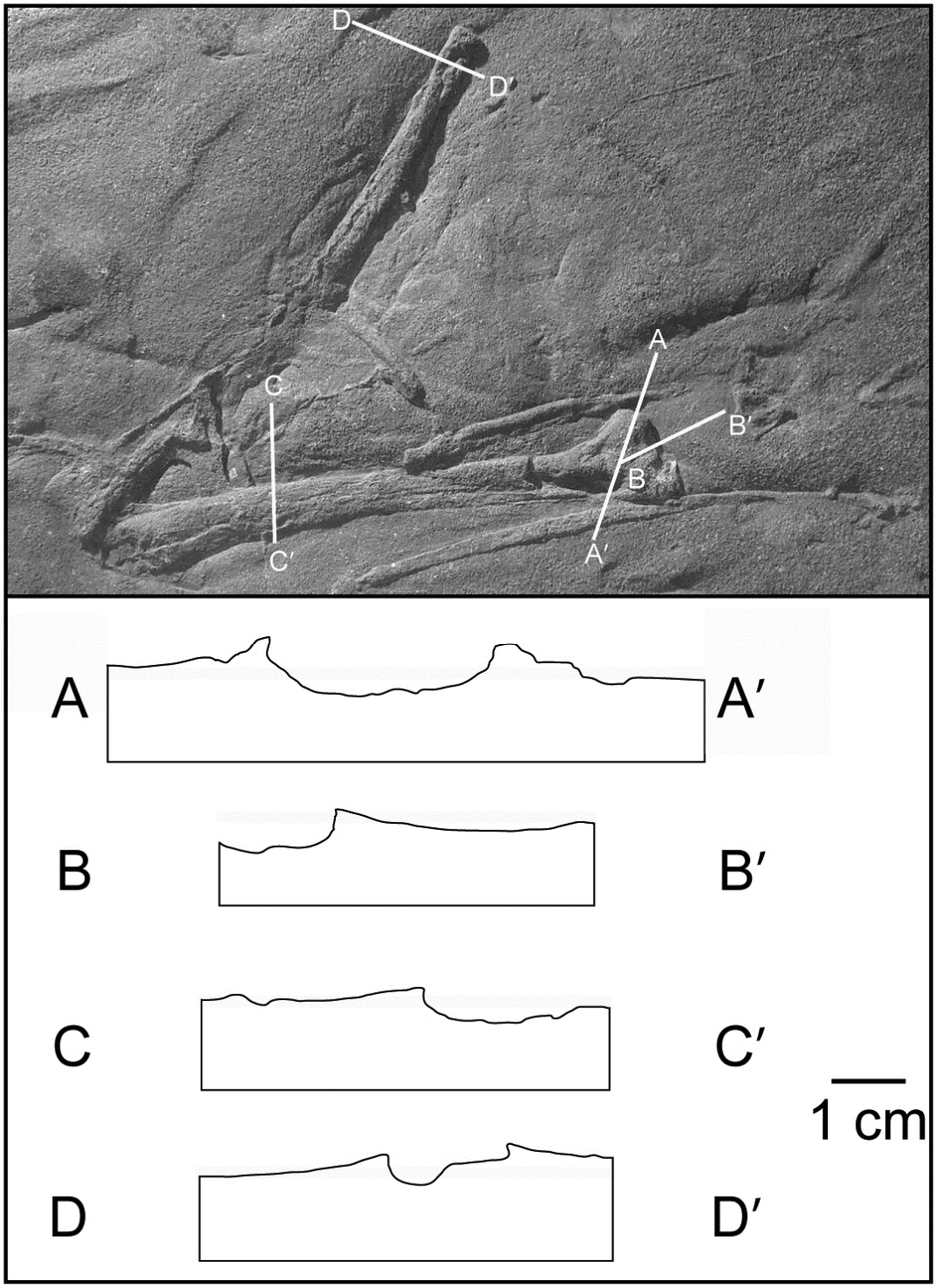

d
lp
A
B
C

Figure 5. Cross-sectional profiles of the bone casts; these replicate the original topography of the muddy substrate underlying the bones. Lines superimposed on bone casts indicate the location of cuts through plaster replicas. Note the crater-like rims of sediment that surrounded and slightly overlapped the bones, especially around the proximal pubis (A to A´, B to B´, and D to D´). Had the bones been removed by current scouring, the rims of sediment should have been damaged. The presence of these rims, along with the fine details preserved within the molds (Fig. 4) suggests that the bones remained in place and were dissolved after burial.


D
D′
A
B′
B
C
C′
A′
A
A′
B
B′
C
C′
1 cm
D
D′

Were Early Jurassic Dinosaurs Gregarious? Reexamining the Evidence from Dinosaur Footprint Reservation in Holyoke, Massachusetts

1. Introduction

Our understanding of dinosaurs has changed radically since the "Dinosaur Renaissance" of the 1970s (see Bakker, 1975). Before that time, these animals were considered evolutionary dead-ends which gave way to the more advanced mammals after the end-Cretaceous extinction event. However, as Bakker pointed out in his analysis of such disparate lines of evidence as bone histology and predator-prey ratios, many dinosaurs appear to have been much more like the mammals in terms of their metabolism than had been previously thought. At the same time, our view of the social lives of dinosaurs also changed. No longer were they viewed as solitary animals, rather, many became viewed as social or gregarious animals. But what evidence is there that we should change our view of dinosaurs and their social lives?

First, we must more define what it means to be gregarious. Gregariousness is the tendency of some animals to gather into structured social groups for a common purpose, such as greater defense against predators, increased access to food, increased breeding efficiency, protection and rearing of young, or increased migration efficiency (Currie and Eberth, 2010). As Ostrom (1972) pointed out, not all natural accumulations of animals constitute a gregarious assemblage. For example, frogs in a pond are not gregarious because the pond dictates where the animals live. Typically, for living animals, the social interactions inherent in gregarious behavior are obvious. For extinct animals, however, gregariousness can only be inferred from their fossil record. Where body fossils (e.g., bones and teeth) are abundant, gregarious

behavior is often inferred from deposits consisting of a single taxon, called monospecific bone beds (Horner, 2002). Unfortunately, many regions, such as the Late Triassic- through Early Jurassic-aged Hartford Basin of Connecticut and Massachusetts (Fig. 1) are nearly devoid of body fossils due to the effects of soil and groundwater chemistry (McDonald, 1992,1995; Getty and Bush, 2011).

In places with a depauperate body fossil record, trace fossils—such as footprints and trackways—may be used as a proxy for skeletal material and can be used to infer gregarious behavior. Indeed, trace fossils may be better indicators of gregariousness than body fossils since they are sedimentary structures that reflect the behavior of the living animals. In contrast, bone beds may result from other factors, including serial predation (predators killing their preferred prey species in the same location over time) and postmortem sorting and accumulation by biological or sedimentological processes (Rogers and Kidwell, 2007).

Gregariousness may be inferred from trace fossils by a suite of characteristics (Lockley, 1991). Among the most obvious of these is trackway parallelism, since herding animals will leave nearly parallel trackways as the herd moves from place to place. Indeed, Edward Hitchcock, in his seminal studies of fossilized footprints, considered parallel trackways as evidence of gregariousness as early as 1836 (see historical account, below). However, parallel trackways also may result from animals walking next to a physical barrier, such as a shoreline (e.g., Ostrom 1972; Lockley, 1991). Since physical barriers can create the illusion of group behavior by funneling animals along a predetermined path, other criteria must also be considered. These other criteria include the constant spacing between both straight and turning trackways that results from members of a group walking next to each other without colliding (Currie, 1983). Additionally, similar speeds calculated from trackways can also be used as

evidence for group behavior since the animals will tend to move at the roughly the same velocity in order to remain in a coherent group (Martin, 2006, p. 433). Finally, because track depth will vary with time (tracks made in wet mud will be deeper than those made in the same substrate after it has dried in the sun a while), depth may be used to infer or reject hypothesized gregariousness (Lockley, 1991). Thus, Getty (2005, p. 173) rejected the hypothesis that two trackways of carnivorous dinosaurs were made by a group because the nearly overlapping and subparallel trackways had significantly different depths and preservational quality.

Based on both body and trace fossil evidence, examples of gregariousness are now known in many groups of herbivorous dinosaurs, including ankylosaurs (e.g., McCrea and Currie, 1998; McCrea, 2000), ceratopsians (e.g., Currie and Dodson, 1984; Lockley and Hunt, 1995; Ryan et al., 2001; Qi et al., 2007), ornithopods (e.g., Cotton et al., 1998; Scherzer and Varricchio, 2010), and sauropodomorphs (e.g., von Huene, 1928; Bird, 1944; Lockley et al., 2002; Castanera et al., 2011). Additionally, gregariousness has been inferred for carnivorous dinosaurs, the theropods, but it has been more controversial, with some researchers supporting the hypothesis (e.g., Currie and Eberth, 2010) and others challenging it (e.g., Roach and Brinkman, 2007). The main thrust of arguments such as those put forth by Roach and Brinkman is generally one of degree, with those researchers arguing that carnivorous dinosaurs were unlikely to have formed complex cooperative groups for the takedown of large prey. Instead, they argue that theropod dinosaurs were more like most modern diapsid reptiles (the group to which dinosaurs belong), which tend to form only loose associations during feeding.

The focus of our field trip is Dinosaur Footprint Reservation (DFR) in Holyoke, Massachusetts, the site from which Edward Hitchcock first (and unwittingly) proposed gregariousness in dinosaurs back in 1836. This site is often referred to in discussions of

dinosaur social behavior, but the evidence remains controversial for some because the tracks are almost universally accepted as having been produced by large, approximately 6 m long, carnivores (e.g., Olsen et al., 1998; Smith and Farlow, 2003; Rainforth, 2005; Lucas et al., 2006, but see Weems, 1987, 1992 for a dissenting opinion). Additionally, ripple marks suggest the presence of a nearby shoreline at the site, but previous arguments for gregarious behavior have either not taken these structures into account or simply dismissed them (e.g., Hitchcock, 1836, 1848, 1858; Ostrom 1972). Thus, the details of the dinosaurs' interactions with their environment have yet to be fully explored. The purpose of this field trip is to reexamine the evidence for gregarious behavior at DFR by integrating the footprint and sedimentological evidence available at the site.

2. Historical Account

Edward Hitchcock first described dinosaur footprints at what is now DFR in 1836. A large track that Hitchcock collected from the locality (specimen number 15/3 at the Beneski Museum of Natural History, Amherst College) was designated as the type specimen of the ichnospecies *Ornithichnites giganteus* (the tracks are now called *Eubrontes giganteus*, see taxonomic discussions in Olsen et al. [1998] and Rainforth [2005]). Hitchcock also noted that four *O. giganteus* trackways were oriented in the same direction and nearly paralleled each other, which he argued was an indication of group behavior in the trackmakers. However, he believed that birds or bird-like animals made the tracks, later citing the discovery of *Archaeopteryx* for support (Hitchcock 1865). (Cope [1867a,b, 1870] first argued that Connecticut River Valley footprints were those of dinosaurs).

When first described by Hitchcock in 1836, *E. giganteus* trackways were known only from DFR. However, he continued to find additional examples, reporting *E. giganteus* at six localities in 1848 and at least eleven localities in 1858. He continued to argue for the gregarious nature of the trackmakers, and although he suggested that additional sites preserved parallel trackways (1848, p. 170), the only specific example provided was DFR, at which the exposure appears to have been enlarged by 1858 based on his description of "several" parallel trackways that were intersected by others. Interestingly, Hitchcock suggested that the animals must have been traveling obliquely to the shoreline, but he did not say why he thought a shoreline was present. Neither did he discuss the possibility that the shoreline may have affected the animals' direction of travel.

After Hitchcock's death in 1864, local geologists continued to cite the parallel trackways at DRF as evidence of gregarious behavior (e.g., Bain and Meyerhoff, 1963), but most workers on Hartford Basin dinosaur tracks (e.g., Lull, 1915, 1953; Olsen and Padian 1986; Olsen et al., 1998; Olsen and Rainforth, 2003; Rainforth, 2003) focused their efforts on much-needed revisions to Hitchcock's taxonomy. However, in 1960s, the trackways at DFR caught the attention of John Ostrom of Yale University, who conducted an in-depth study at the site. Ostrom (1972) identified 22 trackways that he attributed to *E. giganteus*, 19 of which were approximately parallel on a single bedding plane hereafter referred to as the "Ostrom bed." Additionally, Ostrom identified six small theropod trackways oriented in different directions than the much larger *Eubrontes*. Although he noted the presence of ripple marks, Ostrom discounted them as an indicator of a physical barrier because he did not observe any preserved on the main track-bearing bed. Ostrom further argued against the presence of a path-directing physical barrier because smaller theropod trackways were oriented obliquely to the

large theropod trackways. Thus, he concluded that the trackway parallelism, in the absence of a physical barrier, was best explained by gregarious behavior of the trackmakers. Ostrom's study is now entrenched in the literature as an oft-cited example of gregarious behavior (e.g., Colbert, 1989; Lockley and Matsukawa, 1999; Lingham-Soliar et al., 2003).

Recently, some researchers (e.g., Coombs, 1990; Olsen, 2002; Roach and Brinkman, 2007) have revived speculation that the ripple marks indicate a shoreline and have consequently questioned the interpretation that the trackways at DFR represent gregarious behavior, suggesting instead that the parallel trackways represent shoreline-paralleling behavior. However, these authors did not conduct a detailed examination of the site in order to support their arguments. Another study, by Smith et al. (1996), showed that parallel trackways occurred on beds 69 m above the Ostrom bed, suggesting that long term trends affected animal behavior. Finally, Getty (2004) identified numerous herbivorous dinosaur tracks that had not been recognized previously.

3. Geological Context

The Ostrom bed (Fig. 1D) and some of the surrounding land is owned and administered by the Trustees of Reservations as DFR. The reservation, located at 42º 14.5´N latitude, 72º 37.4´ W longitude, is accessible by taking U.S. Rte. 5 north from Holyoke or south from Northampton, Massachusetts. The sedimentary rocks exposed at the outcrops were deposited in the Hartford Basin, an asymmetrical half graben that opened up during the deposition of the Newark Supergroup during the breakup of Pangea in the Late Triassic and Early Jurassic. The rocks at DFR are part of the lower Portland Formation and were deposited in a shallow lacustrine to playa settings (Olsen et al., 1998) in a monsoonal climate strongly influenced by

Milankovich cycling (Olsen, 1986). The Ostrom bed lies almost immediately above the Granby Tuff (Fig. 1B), which crops out on the west side of Rte. 5 to the north and south of the pull-off for the reservation. A 30+ m thick stratigraphic section is discontinuously exposed and extends ~ 100 m to the east, where the youngest beds dip at approximately 13º to the east below the Connecticut River (Fig. 1C, E). Footprints are preserved in virtually all of the exposed beds.

The Ostrom bed consists of gray, fine-grained, micaceous sandstone. Sedimentary structures on this bed include faint (oscillation?) ripples (cf. Ostrom, 1972; Fig. 2A). In many places the Ostrom bed is eroded, exposing a rippled layer approximately 1-2 cm below (Fig. 2B). These ripples are typically straight-crested to slightly sinuous and are symmetric to slightly asymmetric in cross section. Thus, their shape is consistent with oscillatory wave generation, rather than unidirectional currents (Nichols, 1999, p. 54). Similar but more sinuous ripples, occur to the east on a remnant of a bed approximately 13 cm above the Ostrom bed (Fig. 2C-D). Additional structures on the Ostrom bed include elongate and irregularly ovate to circular depressions with a maximum diameter of 2.2 cm (Fig. 2.E). These structures are often called “raindrop impressions”; however, based on their large size and irregular shape, we consider them to be molds of weathered away concretions or pebbles.

Sedimentary structures suggesting subaerial exposure and desiccation are rare. Desiccation cracks occur on a single bed high in the section; none occur on or near the Ostrom bed itself. Raindrop impressions have not been observed on any beds, but rare evaporite pseudomorphs were observed by Bain and Meyerhoff (1963), although these authors did not indicate on which beds the structures were observed.

Besides dinosaur tracks, no other fossils were observed on the Ostrom bed. Fossilized wood is abundant high in the section (Fig. 2F), along with rare examples of vertical *Skolithos* burrows (Fig. 2G). Horizontal burrows are restricted to the rippled layer immediately below the Ostrom bed. These burrows range from 1-5 mm in diameter (Fig. 2B, H) and are of variable length. They are subhorizontal and appear to have a minor vertical component based on their abrupt, yet rounded, terminations. The burrows are concentrated in the troughs of the ripples, although they cross-cut some ripple crests. They are not uniformly distributed across the surface; sediments at the north end of the site are only slightly disrupted (bedding plane bioturbation index 1 of Miller and Smail, 1997, see Fig. 2A), whereas exposures at the south end of the site are more highly disrupted (bedding plane bioturbation index of 3, see Fig. 2H). The concentration of the burrows in ripple troughs suggests that the animals were collecting organic detritus that accumulated in low-lying areas, whereas the greater bioturbation at the south end of the site may reflect a water depth gradient.

Overall, the sedimentology and trace fossils at the site are consistent with a shallow, saltwater aquatic setting with occasional subaerial exposure. The relative rarity of invertebrate bioturbation may have resulted from high salinity in the lakes. Additionally, dysoxic or anoxic bottom conditions may have developed at times if the water became stratified with dense hypersaline water on the shallow lake bottoms. Such conditions have been inferred for the lakes in the underlying East Berlin Formation (Gierlowski-Kordesch and Rust, 1994) and elsewhere in the Portland (Sime and Getty, 2009).

4. Methods

The footprints at DFR were re-examined in the summer of 2010 to test the gregariousness hypothesis for the *Eubrontes* trackmakers and to provide a comprehensive survey of the non-*Eubrontes* tracks at the site. Efforts were first focused on the Ostrom bed, which was divided into two sections (north and south, separated by a large, comma-shaped, vegetated region) that were examined separately. Footprints were first located and outlined with chalk. Due to the highly weathered nature of most of the footprints, each section was examined during both the morning and late afternoon, when low-angle light struck the surface from different angles. Wherever possible, tracks were identified to the ichnogenus level using the definitions found in Olsen and Padian (1986) for the crocodylomorph track *Batrachopus*, Olsen et al. (1998) for the theropod ichnogenus *Eubrontes*, and Olsen and Rainforth (2003) for the small ornithischian *Anomoepus*. Theropod tracks smaller than *Eubrontes*, such as *Grallator* and *Anchisauripus*, were lumped together and referred to as "small theropod tracks" due to the poor preservation of most examples.

After the footprints were identified, their positions were recorded using a Leica Flexline TS/02 total station. Each footprint was characterized by two points: one proximal (usually the metatarsal-phalangeal pad behind digit four) and one distal (usually the tip of digit three). The data were transferred from the total station into Autocad ® software to produce a preliminary map. The map was then entered into Adobe Illustrator ® to produce a final map on which the dinosaur tracks are represented by idealized outlines for clarity.

Additional data collected in the field included compass bearings for ripple crests, for all *Eubrontes* trackways on the Ostrom bed and on beds examined by Smith et al. (1996), and for all other trackway types in the north end of the Ostrom bed. Compass bearings were measured

by running a tape measure down the midline of the trackway and measuring the orientation of the tape. When necessary, the orientations of isolated tracks were recorded from a line drawn down the middle of the track, through the middle digit. The data were analyzed using PAST ® software.

5. Results

A total of 787 dinosaur tracks, including *Eubrontes*, *Anchisauripus*, *Grallator*, and *Anomoepus* were identified, as was one manus-pes set of the crocodylomorph ichnogenus *Batrachopus* (Fig. 3). This contrasts strongly with the 134 dinosaur tracks reported by Ostrom (1972). The new map of the site can be seen in Figure 4A and the relative proportions of track types at the site is given in Figure 4B. Details for the different track types are discussed below.

The orientation of 106 ripple marks were measured on the bed immediately below the Ostrom bed, four orientations were measured on the Ostrom bed, and 27 were measured on the surface 13 cm above the Ostrom bed. All ripple crest orientations, regardless of bed, show the same east-west trend (Fig. 5A).

A total of 231 *Eubrontes* tracks were identified on the Ostrom bed, almost twice as many as the 117 tracks reported by Ostrom (1972). Assuming that none of the animals walked across the surface more than once, the isolated tracks and complete trackways represent 53 animals. Forty of those tracks/trackways, or 75% of the total, trend approximately to the west (Fig. 5B). Significantly, the other 13 trackways are not randomly oriented either, but are clustered in a group to the east. Thus, the large theropods that crossed the Ostrom bed have two preferred orientations approximately 180º apart. Regardless of direction of travel, most of the *Eubrontes* trackways are relatively straight or meander only slightly. However, a single trackway appears

to show an animal stopping and then taking a turn to the right (Figs. 3I-J, 4A, arrowed trackway).

In addition to the *Eubrontes* on the Ostrom bed, 49 *Eubrontes* trackways were identified on 20 beds by the Connecticut River, and bearings were recorded for these as well. These data were combined into a single rose diagram (Fig. 5C) because most beds had only one trackway. The combined data show a similar trend to the Ostrom bed, with many trackways headed to the west and fewer trackways headed to the east. However, the trackway orientations are more widely distributed, with some trackways headed to the northeast and northwest. None, however, are oriented to the south. Significantly, a few trackways within a few meters of each other are nearly parallel.

A large number of other tracks were identified on the Ostrom bed, most of which had not been previously reported. These include 248 small theropod (both *Grallator* and *Anchisauripus*) tracks, 205 *Anomoepus* tracks, 103 unidentified tracks, and a single crocodylomorph manus-pes track set attributable to *Batrachopus*. Again assuming that no animal crossed the track surface more than once, these trackways represent 197 small theropods, 127 ornithischian herbivores, and a single crocodilian. Orientations of 86 smaller theropod trackways at the north end of the site show a statistically significant ($p < 0.05$, Chi squared test) northwest-to-southeast trend (Fig. 5D). The 44 *Anomoepus* trackways at the north end of the site show greater trackway concentrations to the east and west. However, *Anomoepus* trackways also trend to the north and south, and neither Chi-squared nor Raleigh tests indicated statistically significant non-random distributions (Fig. 5E). As Getty (2004) noted, a single *Anomoepus* trackway bears a long, sinuous tail drag (Figs. 3K-L, 4A).

6. Discussion

Ostrom (1972) reported that ripple marks did not occur on the bed that he mapped, and therefore he rejected these structures as indicating a physical barrier (i.e., shoreline) at the site. However, faint ripples do in fact occur on the Ostrom bed. More significant than these poorly defined ripples is that fact that well-developed oscillation ripple marks occur only 1-2 cm below and 13 cm above the Ostrom bed, and that all of the ripples have similar orientations to the northeast and southwest. Considering that oscillation ripples tend to form subparallel to the shoreline (Johnson and Baldwin, 1996, p. 263), and that ripple crests of the same general orientation occur below, on, and above the Ostrom bed, it is reasonable to assume that the general trend of the paleoshoreline at DFR was also from the northeast to southwest, at least during the deposition of those beds. Thus, it is conceivable that the shoreline acted as a physical barrier that constrained the dinosaurs' movement at this site.

A bimodal distribution is considered strong evidence of shoreline-paralleling behavior (Lockley, 1986). The fact that the bimodal distribution at DFR encompasses all of the *Eubrontes* trackways on the Ostrom bed, with the two trends approximately paralleling the inferred shoreline, strongly suggests that the shoreline did in fact dictate which direction these large theropods traveled. This assertion is reinforced by the similar east-west trend of many of the *Eubrontes* trackways at the top of the section (Smith et al., 1996; thus study). Bimodality is not as pronounced for these trackways, but this is not surprising considering that shoreline patterns may have changed in the time that it took for the intervening beds to be deposited. Although many beds higher in the section do show ripple crest trends to the east and west, there is more variation in orientation among beds (personal observations), and thus there may have been many minor changes in shoreline orientation. Further, the depositional setting appears to

have changed slightly higher in the section. Rare mud cracks suggest that desiccation may have been greater higher in the section, and *Skolithos* burrows, which are known only in playa settings in the underlying East Berlin Formation (Gierlowski-Kordesch, 1991), have been identified.

Although the data from the Ostrom bed strongly supports the hypothesis that the animals were engaging in shoreline-paralleling behavior, this alone does not falsify the hypothesis that the animals were gregarious because, as Lockley (1991) has pointed out, shorelines will direct groups of animals in the same way that they direct individuals. Some lines of evidence seem to support the gregariousness hypothesis, whereas others don't. For example, most of the trackways for which velocities have been calculated indicate relatively slow, steady progression (Lepore, 2006), which could indicate gregariousness. Additionally, three nearly parallel and overlapping trackways (including the animal that turns, see fig. 4A) traverse the site oblique to the orientation of all the trackways that they cross. These trackways may represent a small group of animals that crossed the surface at the same time.

From an ecological perspective, Weems (1987, 1992, 2003) argued that gregariousness in the dinosaurs at DFR would have been unlikely if they were theropods because the animals were larger than their potential prey items (the tracks of large prosauropods, such as *Otozoum*, are never found in association with *Eubrontes* tracks, from which it is inferred that these animals occupied different habitats [Rainforth, 2003]), and because potential prey left fewer footprints in the Hartford Basin, suggesting that they were rarer (e.g., see Wright, 1997). Traveling in large groups, therefore, would have been disadvantageous because any individual would have to have shared its prey with its cohorts, thereby decreasing its potential food intake. Weems accepted at face value that the dinosaurs at DFR were gregarious, and argued instead

that gregariousness indicated the trackmakers were herbivores. While we reject the contention that the *Eubrontes* trackmaker was an herbivore, as have most other researchers based on osteological comparisons of the tracks to skeletal material, we note that the argument put forth by Weems has some merit and we suggest that the theropods crossed the Ostrom bed as isolated individuals, or at most in small groups. Further research, outlined in the following section, is designed as an additional test the hypothesis that the *Eubrontes* trackmaker was gregarious.

The orientations of the trackways of other dinosaurs at DFR are quite interesting—smaller theropod trackways are preferentially oriented northwest and southeast, offset from both the ripple crest and *Eubrontes* orientations. If this trend proves to be consistent on the south end of the site, it may indicate that small and large theropods utilized the ecosystem differently. Specifically, movement towards and away from the water may support the hypothesis that Early Jurassic theropod-dominated faunas were based on piscivory, as proposed by Olsen (2010) for the Hartford Basin and Milner and Kirkland (2007) for the St. George Dinosaur Discovery Site in Utah. The more random orientation of the herbivorous ornithischians suggests that the lake was not as important at defining their patterns of movement as it was for carnivores.

7. Conclusions and Future Work

The dinosaur tracks at Dinosaur Footprint Reservation in Holyoke, Massachusetts have been re-examined for evidence of gregarious behavior in the light of sedimentary structures present at the site. Oscillation ripple mark crest orientations below, on, and above the main Ostrom bed were used to constrain the approximate shoreline orientation, which was

approximately northeast to southwest. *Eubrontes* tracks preserved on the Ostrom bed represent 53 large theropods exhibiting a bimodal distribution oriented approximately to the east and west, roughly parallel to the inferred shoreline. This distribution, along with evidence that the distribution continues on surfaces stratigraphically above the Ostrom bed, strongly suggests that the physical barrier produced by the shoreline dictated the orientation of these animals' movement. Trackways analyzed to date indicate that smaller theropods trended oblique to the shoreline and that small herbivores show no strong preferred orientation. The orientations of small theropods relative to the shoreline may support the hypothesis that the Early Jurassic dinosaur fauna of the Hartford Basin was based on piscivory.

Shoreline-parallel behavior by the *Eubrontes* trackmakers does not falsify the hypothesis that the animals were gregarious, since a physical barrier will direct the orientations of groups just as it directs the paths of individuals. The gregariousness hypothesis can be further tested by considering whether parallel *Eubrontes* trackways occur at other localities and in other sedimentary facies in which such physical barriers as shorelines were transient or absent altogether. Framed in this way, the absence of parallel trackways in other sedimentary environments, such as playa-lake facies, would constitute strong evidence that the parallel trackways at DFR are a facies-specific accumulation rather than evidence of gregariousness. Significantly, detailed studies at Dinosaur State Park in Rocky Hill, Connecticut by Ostrom (1972) and Farlow and Galton (2003) have failed to find a preferred orientation in the *Eubrontes* trackways at that site. We are currently examining additional sites to test the facies specificity of parallelism in *Eubrontes* trackways.

Road Log:

Time to arrival at stop: 40 minutes.

0.0 Trip begins outside of the Hartford Marriot Downtown, at 200 Columbus Blvd. Hartford, CT 06103

0.03 Heading north on Columbus Blvd., turn left onto Grove St.

0.05 Turn right at fork and merge onto I-91 N.

34.7 Take exit 17A to merge onto MA-141 E (Easthampton Rd) toward Holyoke.

0.5 Turn left onto US Rte. 5 (Northampton St).

2.2 Pull off into parking area at destination.

0.0 Turn left out of parking area to head on US Rte 5 south (Northampton St).

2.0 Turn right onto Hampden St

0.2 Merge onto I-91 S via ramp to the left

34.8 Take exit 31 for State St

0.3 Merge onto CT-2 W

0.02 Turn left onto Columbus Blvd

0.1 Hotel will be on the left

Total mileage: 74.9

Figure 1. Location and geologic context of Dinosaur Footprint Reservation (DFR). (A) Bedrock geology of the northern portion of the Hartford Basin. The star indicates the location of DFR within the basin. (B) Simplified stratigraphic column of Hartford Basin rocks showing the position of DFR immediately above the Granby Tuff. (C) Google Earth image of the land surrounding DFR. Note the position of DFR immediately to the east of U.S. Rte. 5 and additional outcrops along the west bank of the Connecticut River (labeled "beds by river." (D) Oblique view of the "Ostrom bed" at DFR. E: View to the south of beds cropping out along the Connecticut River. These beds, which are not part of the reservation, also preserve dinosaur tracks. Panels (A) and (B) modified from Collette et al. (2011) and reproduced with permission of Atlantic Geology.

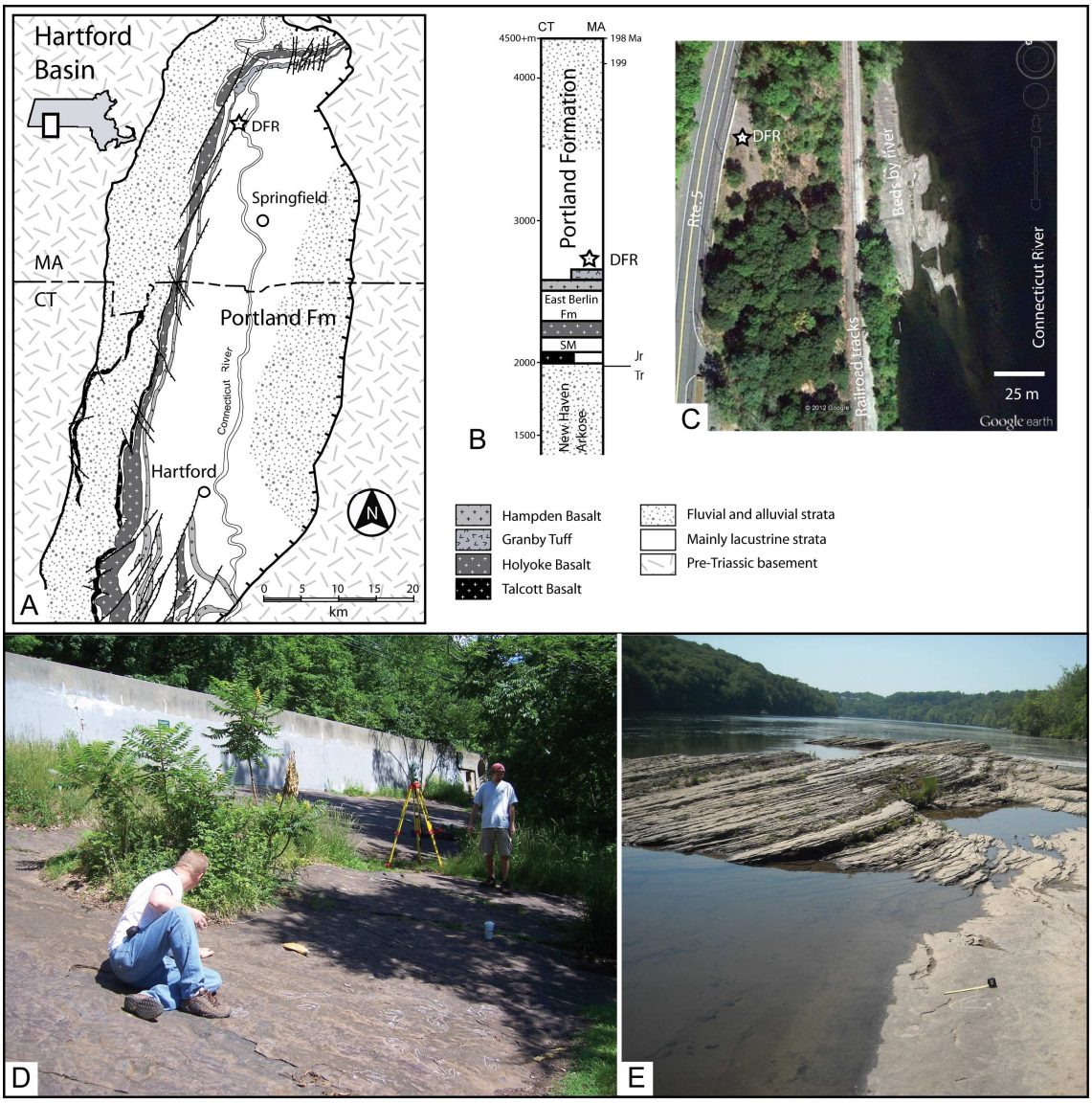
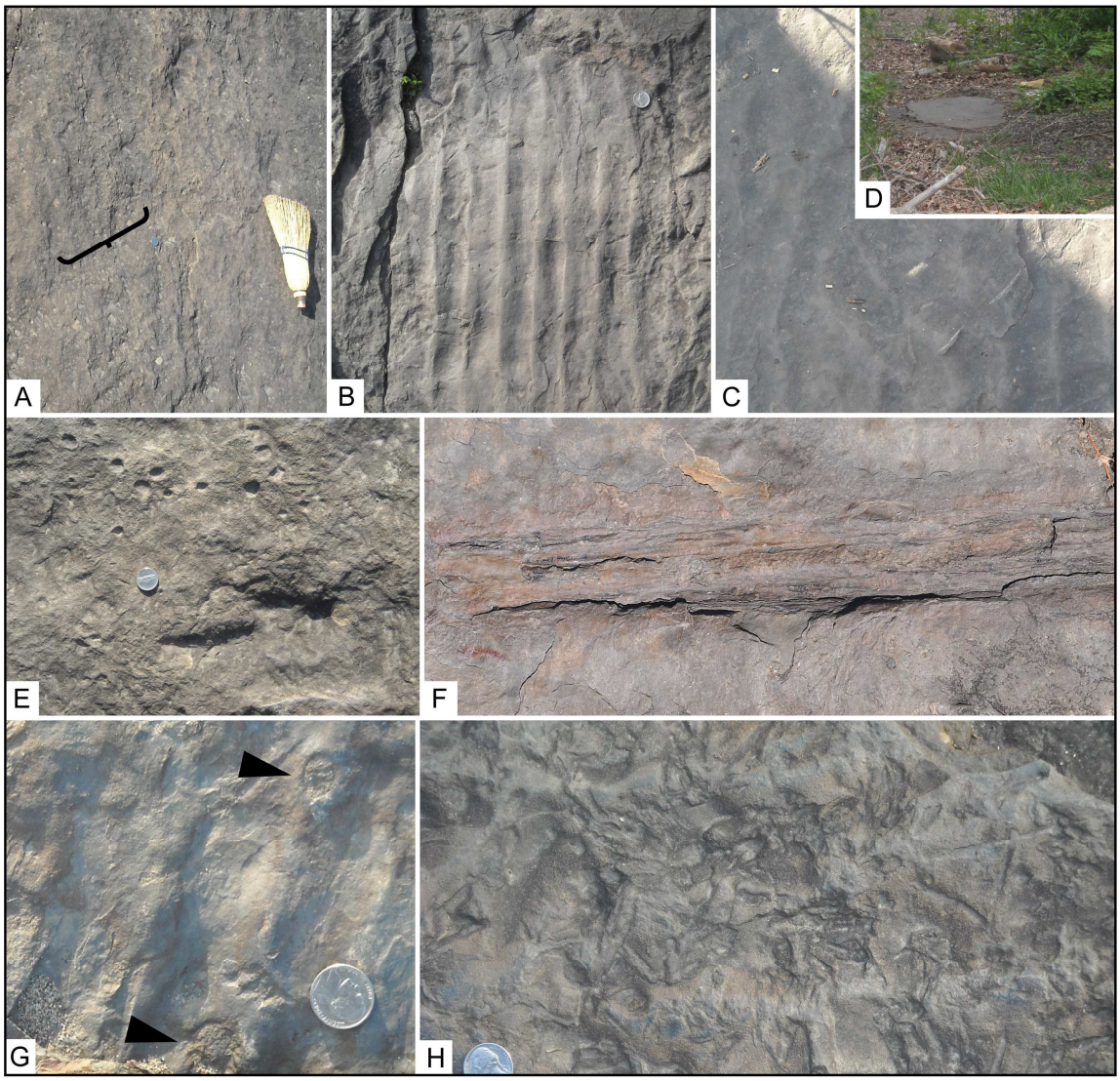

Hartford Basin
DFR
Springfield
MA
CT
Portland Fm
Connecticut River
Hartford
N
0 5 10 15 20
km
A
CT MA
4500+m
198 Ma
199
4000
Portland Formation
3000
DFR
East Berlin Fm
SM
2000
Jr
Tr
New Haven Arkose
1500
B
DFR
Rte. 5
Beach by river
Railroad tracks
Connecticut River
25 m
Google earth
C
Hampden Basalt
Granby Tuff
Holyoke Basalt
Talcott Basalt
Fluvial and alluvial strata
Mainly lacustrine strata
Pre-Triassic basement
D
E

Figure 2. Sedimentary structures and non-vertebrate fossils from DRF and the surrounding area. (A) Poorly preserved ripple marks on the Ostrom bed are indicated within the bracketed region. (B) Well-developed, straight to slightly sinuous oscillation ripples are preserved on a bed discontinuously exposed 1-2 cm below the Ostrom bed. This photograph was taken at the north end of the site, where few horizontal burrows are preserved. (C) Sinuous ripples preserved on a bed 13 cm above the Ostrom bed. (D) View looking to the east from the Ostrom bed showing the remnant layer on which the ripples in C are preserved. (E) Ovate pits on the Ostrom bed. Note the theropod track below and to the right of the coin. (F) Fossilized wood is preserved on multiple beds by the Connecticut River. Field of view in this image is approximately 0.8 m. (G) *Skolithos* burrows, indicated by arrowheads, occur on some beds by the river. (H) The same rippled bed as in (C). This exposure, from the south part of the site, shows intense bioturbation concentrated in the troughs of ripples. Scales: coin = 2.1 cm; whisk broom = 28 cm.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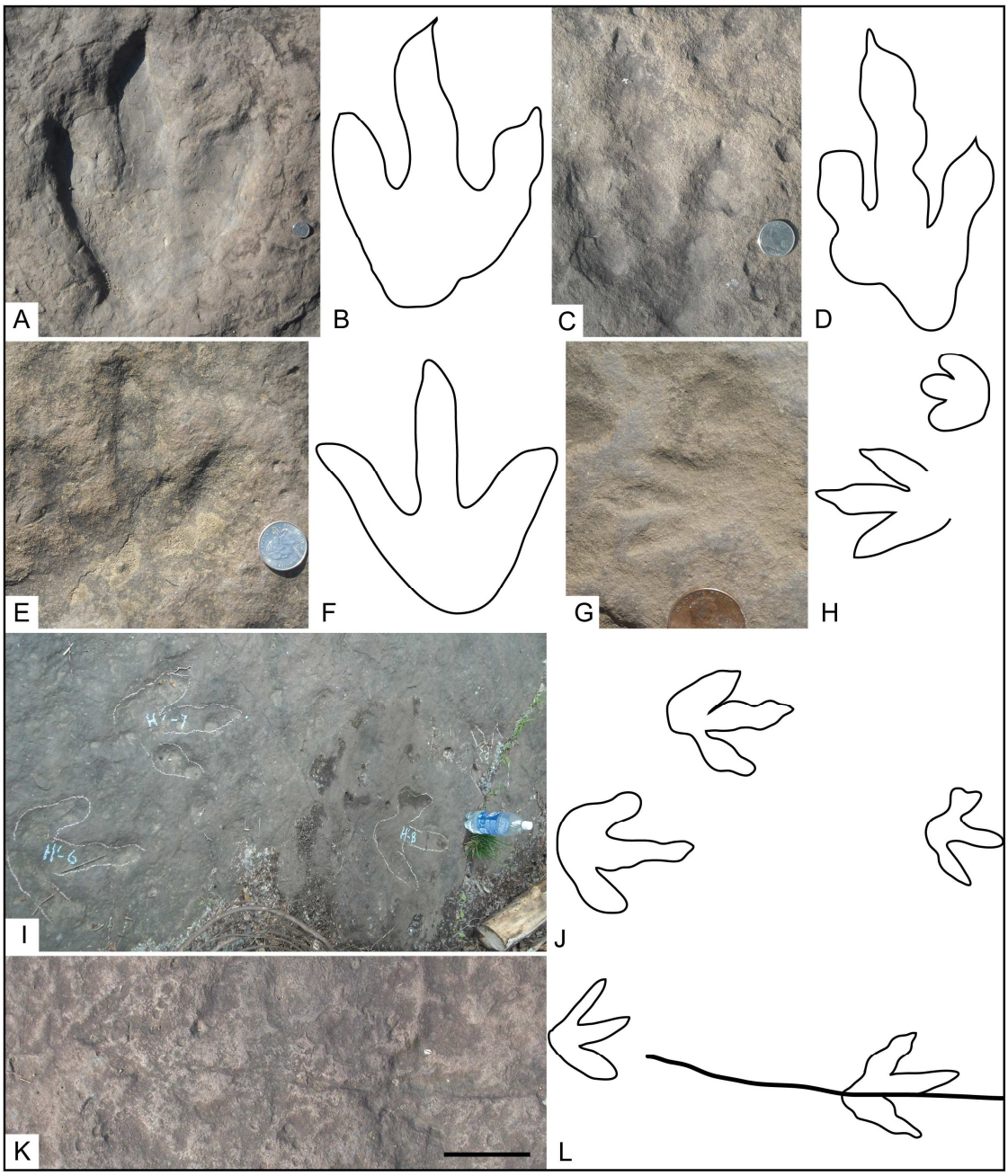
G
H

Figure 3. Vertebrate trace fossils preserved on the Ostrom bed. (A) *Eubrontes giganteus* track, produced by a large theropod. (B) Interpretive drawing of (A). (C) Smaller theropod track (*Anchisauripus* isp.). Note the pads on the toes. (D) Interpretive drawing of (C). (E) *Anomoepus scambus* track, produced by a small herbivorous ornithischian. Note the wide angle between the toes, stubby middle digit, and blunt claws that are characteristic of this ichnospecies. (F) Interpretive drawing of (E). (G) A single manus-pes set attributable to the crocodylomorph ichnogenus *Batrachopus*. The manus is smaller and at the top of the image; the pes is larger and at the bottom. The pes is missing the first digit. (H) Interpretive drawing of (G). (I) Oblique view of the turning *Eubrontes* trackway. (J) Interpretive drawing of (I). (K) Close-up of the *Anomoepus* trackway with a trail drag. (L) Interpretive drawing of (K). Coin in (A) = 2.1 cm, in (C) and E = 2.4 cm, and in (G) = 1.9 cm, bottle in approximately 20 cm tall, scale bar in (K) is 10 cm.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L

Figure 4. Details of the dinosaur tracks from the Ostrom bed. (A) Color-coded map showing all 787 dinosaur tracks identified. The position, size, and orientation of individual tracks are accurate, but idealized track symbols were used for clarity at this scale. The long green line indicates the position of an *Anomoepus* tail drag. Also note the bent arrow on the track surface, which indicates the position and direction of movement of a large theropod that stopped and then turned to the right. The small star in the lower right of the map indicates the position of the *Batrachopus* manus-pes set. (B) Relative proportions of trackmakers. These data were calculated as the number of individuals per taxon, assuming that each trackway and isolated footprint was produced by a unique individual, divided by the total number of individuals across taxa.

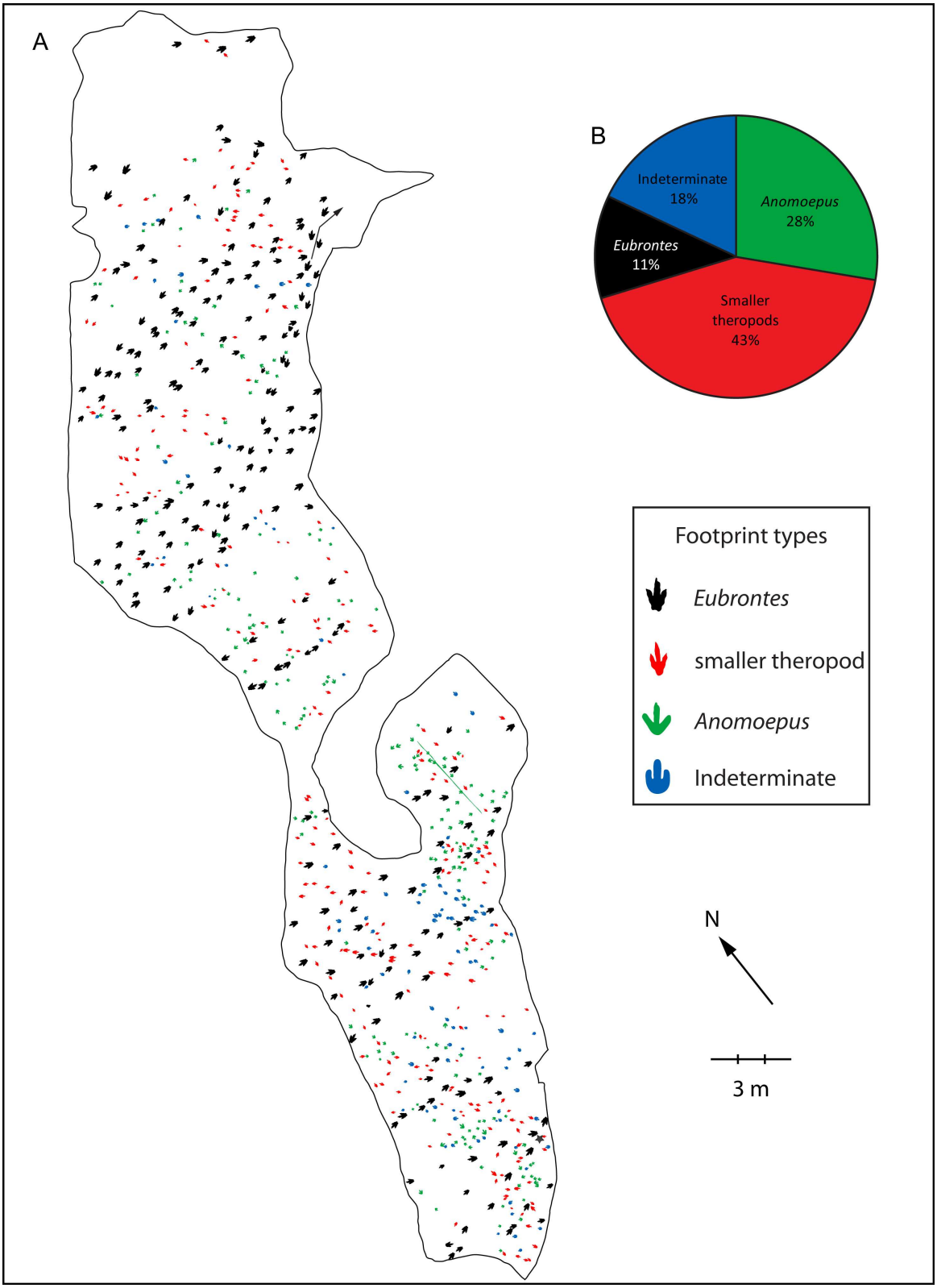
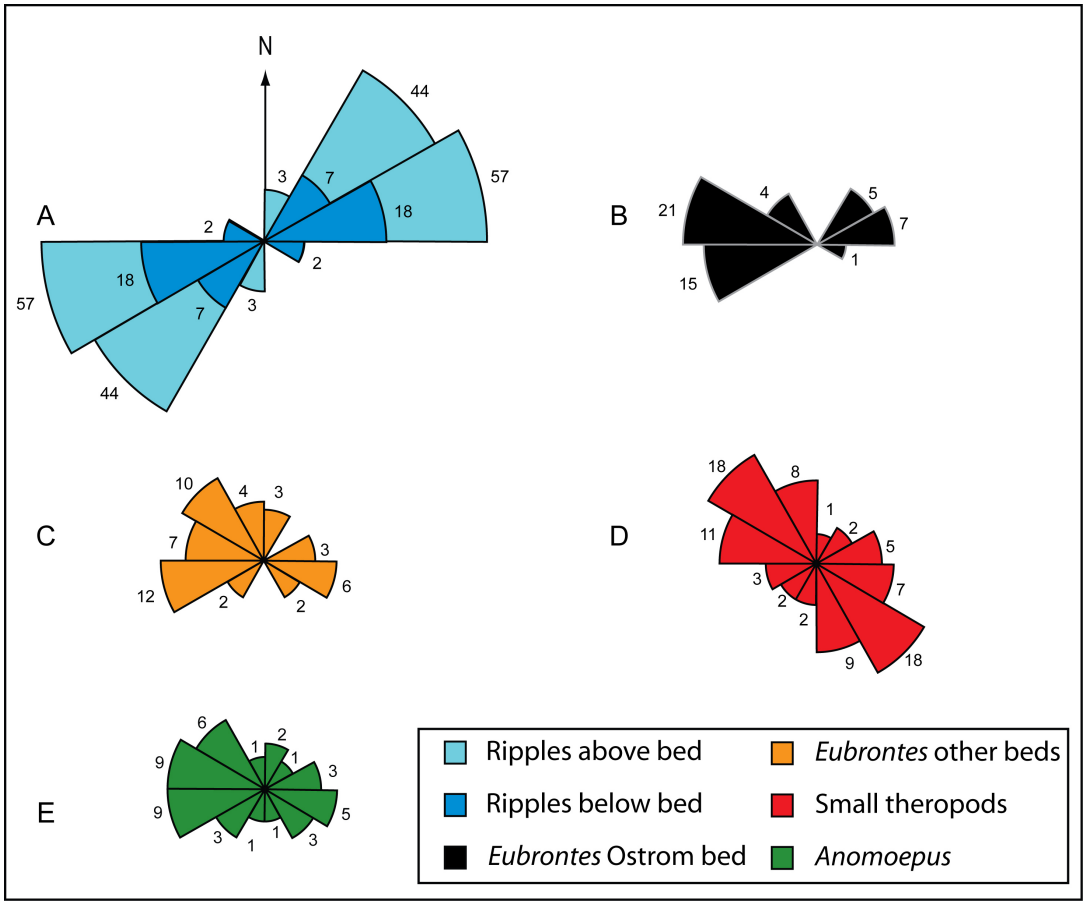

A
B
Indeterminate
18%
Anomoepus
28%
Eubrontes
11%
Smaller
theropods
43%
Footprint types
Eubrontes
smaller theropod
Anomoepus
Indeterminate
N
3 m

Figure 5. Equal area rose diagrams of ripple and track orientations. (A) Orientations of ripples below and above the Ostrom bed. Note that the two sets of data overlap and suggest a northeast-southwest trend to the paleoshoreline. (B) Orientations of *Eubrontes* trackways on the Ostrom bed. Note the bimodal distribution with the two groupings nearly 180º offset. Note also that these groupings are trend to the east and west, approximately parallel to the shoreline. (C) *Eubrontes* orientations from 20 beds by the Connecticut River (upsection from the Ostrom bed). Note the bimodal distribution toward the east and west. The trend is less strong due to the amalgamation of multiple beds and changes in shoreline orientation higher in the section. (D) Distribution of small theropod (*Anchisauripus* and *Grallator*) tracks on the northern part of the Ostrom bed. Note the strong bimodality that is oriented oblique to the shoreline. (E) Orientations of *Anomoepus* tracks on the Ostrom bed. Greater numbers of trackways are oriented to the east and west; however, trackways are oriented north and south as well, and bimodality was not statistically significant.


N
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C
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5
3
7
2
2
9
18
E
6
2
9
1
1
3
9
5
3
1
1
3
Ripples above bed
Ripples below bed
Eubrontes Ostrom bed
Eubrontes other beds
Small theropods
Anomoepus

Variation in wingless insect trace fossils: insights from neoichnology and the Pennsylvanian of Massachusetts

ABSTRACT

Trace fossils of basal, apterygote (wingless) insects from the Pennsylvanian-aged Rhode Island Formation of southeastern New England include the body imprint *Tonganoxichnus buildexensis* and the trackways *Mitchellichnus ferrydenensis*, *Siskemia elegans*, *Stiallia pilosa*, and *Stiaria intermedia*. Trackways with double- and triple-medial impressions (*S. elegans* and *M. ferrydenensis*) are rare among trace fossils attributed to such insects. To determine how these unusual trackway morphologies were produced, and why they are so rare, experiments were conducted over a range of substrates with modern archaeognathans (jumping bristletails) and thysanurans (silverfish). Our experimental results suggest that archaeognathans produced the fossil body imprints, as well as trackways exhibiting opposite symmetry, but cannot rule out thysanurans for trackways exhibiting alternate symmetry. The results also show that a variety of appendages leave medial impressions. The rarity of fossil trackways with more than one medial impression results from the animals' low mass and the delicate nature of the appendages making such structures, coupled with behavior (jumping and landing) and substrate properties (saturation and cohesiveness). The production of different numbers of medial impressions by a single archaeognathan species suggests that fossils should show similar variety, albeit in rare cases, and that the named ichnotaxa are likely derived from a single biological taxon. Finally, the experimental work provides new insights into the production and preservation in *Stiallia* and *Tonganoxichnus*.

1. Introduction

Archaeognathans (Figs. 1A and B) are an order of apterygote (wingless) insects that constitute the sister group to all other insect lineages (Grimaldi and Engel, 2005; Regier et al., 2010; Fig. 1E). The order includes the extinct Monura (Fig. 1C) as well as two extant families known together colloquially as jumping bristletails (Bitsch and Nel, 1999; Grimaldi and Engel, 2005; Rasnitsyn, 2002; Bechly and Stockar, 2011; Figs. 1A-B). The body fossil record of the Archaeognatha is sparse, but fragmentary remains have been found that are as old as the Early to Middle Devonian (Shear et al., 1984; Labandeira et al., 1988). Monurans have a stratigraphic range that extends from the Late Carboniferous through the Middle Triassic (Bechly and Stockar, 2011), and unequivocal examples of modern archaeognathan families are known from amber of Cretaceous and younger age (Grimaldi and Engel, 2005).

Trace fossils, including body impressions (*Tonganoxichnus*) and trackways (*Stiaria* and *Stiallia*), supplement the body fossil record (Table 1). Despite some disagreement (see discussion), *Tonganoxichnus* is generally attributed to the Archaeognatha based on a number of characteristics. For example, the traces exhibit three-part tagmatization (inferred to represent the head, thorax, and abdomen), with three pairs of leg impressions on the thorax—a defining feature of hexapods (Bitsch and Bitsch, 2004). The traces also exhibit long furrows in the head region that are inferred to have been made by elongate maxillary palps, modified organs that are diagnostic of archaeognathans (Bitsch and Bitsch, 2004; Bechly and Stockar, 2011). Finally, imprints of pointed distal tarsi and abdominal styli, combined with evidence for jumping inferred from some of the traces, also suggest an archaeognathan trace maker (Buatois et al., 1997, 1998; Mángano et al., 1997, 2001; Braddy and Briggs, 2002; Minter and Braddy,

2006a). Four species are included within the ichnogenus *Tonganoxichnus*: *T. apacheensis* (originally included in *Hedriumichnus* by Braddy and Briggs [2002], but later synonymized with *Tonganoxichnus* by Minter and Braddy [2009]), *T. buildexensis*, *T. ottawensis*, and *T. robledoensis* (Mángano et al., 1997; Braddy and Briggs, 2002; Minter and Braddy, 2006a, 2009). Recently, Benner et al. (2011) noted *Tonganoxichnus* from the Wamsutta Formation of Massachusetts.

The presence of *Stiaria intermedia*, which is composed of a single medial impression and series of one to three imprints arranged in alternate to opposite symmetry, on the same beds as *T. ottawensis* (Mángano et al., 1997, fig. 5; Buatois et al., 1998, fig. 8), suggests that both traces were made by the same archaeognathan insect, and the discovery of *S. intermedia* leading up to and away from the jumping trace *T. robledoensis* (Minter and Braddy, 2006a) further supports this contention. Another feature of some *S. intermedia* that may indicate an archaeognathan producer is opposite symmetry of the track series. Although many arthropods employ oppositely symmetric locomotion (e.g., Briggs and Rolfe, 1983), among extant hexapods only archaeognathans can do so (Manton, 1977, plate 6f). (Other modern insects use the hexapod gait, wherein opposing legs are used alternately.) A third trace, called *Stiallia pilosa*, consists of two rows of closely spaced grooves and has also been tentatively assigned to the Archaeognatha when it co-occurs with *Tonganoxichnus* and *Stiaria*. It is generally considered a combined feeding and locomotion trace (Buatois et al., 1998).

Stiallia, *Stiaria*, and *Tonganoxichnus* (as well as *Mitchellichnus* and *Siskemia*, see below) from Plainville, Massachusetts extend geographically the trace fossil record of archaeognathan insects to the Pennsylvanian-aged Rhode Island Formation of the Narragansett Basin in southeastern New England. However, in addition to the typical *Stiaria* trackway

morphology described above, the Plainville record contains trackways that are unusual in possessing two or three medial impressions; there is only one other trackway known that exhibits a double-medial impression (Buatois et al., 1998, fig. 8.1) and one that exhibits a triple-medial impression (Fillmore et al., 2012, fig. 26). The purpose of this paper is to describe these new archaeognathan trace fossils and to present the results of experimental research that was conducted to determine how the unusual trace morphologies were made and preserved.

2. Geological and Paleontological Context

The Narragansett Basin (Fig. 2) is a composite rift basin that formed as small grabens coalesced during the collision between the Avalon microcontinent and Laurentia during the Paleozoic (Mosher, 1983). The basin filled with terrestrial sediments, producing conglomerate, sandstone, siltstone, shale, and coal. Depositional environments include alluvial fans, braided and meandering streams, floodplains, and swamps (Mosher, 1983, and references therein). Until recently, basin formation was thought to have been continuous, starting in the Pennsylvanian, but radiometric dating suggests that crustal extension began as early as the Late Devonian, ca. 373 Ma (Maria and Hermes, 2001; Thompson and Hermes, 2003).

The fossils discussed here were collected from a large, open-pit quarry that exposes Middle Pennsylvanian-aged rocks of the Rhode Island Formation, which are ca. 312-314 Ma (P. Lyons, personal communication, 2009). The quarry walls are composed of shale, coal, and sandstone that were deformed and metamorphosed in the Permian (ca. 290-280 Ma) as Africa and North America collided during the building of Pangea (Lyons and Chase, 1976; Skehan et al., 1979; Dallmeyer, 1982; Mosher, 1983; Lyons, 1984). Rocks in the northern part of the

basin, where Plainville is located, experienced deformation that produced northeast to east-northeast trending folds with axial planes dipping to the northwest, and mild, lower Greenschist facies metamorphism (Skehan et al., 1979; Mosher, 1983; Murray et al., 2004; Lynn and Kroll, 2006). As a result of the tectonic activity, the Plainville fossils have been modestly deformed, making measurements of their original dimensions difficult to obtain. Thus, the measurements reported here are approximations. As has been done with other deformed fossils (e.g., Wood et al. 2003), a study is underway to retrodeform all of the Plainville trace fossils in order to obtain better measurements (Fichman et al., 2012, 2013).

The shales in which the fossils occur are considered low-energy interchannel, swamp, and floodplain sediments (Towe, 1959; S. Voigt, personal communication, 2010). Mud rip-up clasts have been identified in some layers, indicating that localized erosion took place, and preferred alignment of plant debris indicates that drainage was from the northeast (Lyons and Chase, 1976). Sedimentary structures commonly associated with fossils include desiccation cracks, gas-escape structures, raindrop imprints, and current ripples.

Oleksyshyn (1976) reported two lycopsid, ten sphenopsid, three pteridophyte, and twelve gymnosperm species from the site. Additionally, rhizoliths have been observed in some track-bearing slabs. Animal fossils are restricted to traces, and our preliminary investigations have shown the ichnofauna to be diverse. For example, invertebrates are represented by the arthropod trackway *Umfolozia sinuosa*, the myriapod traces *Diplichnites gouldi* and *Diplopodichnus biformis*, and a probable ephemeropteran body impression. The trails *Gordia marina* and *Helminthoidichites tenuis* are common on bedding surfaces, and *Planolites* burrows have been identified penetrating slabs. Among vertebrates, fish are represented by the trails *Undichna unisulca* and *Undichna* isp.; amphibians by footprints and trackways referred to

Batrachichnus plainvillensis, *Characichnos tridactylus*, and *Limnopus vagus*; and basal reptiles by footprints and trackways referred to *Notalacerta missouriensis* (Getty et al., 2010). These other traces will be described in detail elsewhere.

3. Systematic Ichnology

Specimens described herein are housed in the Invertebrate Paleontology Division of the Yale Peabody Museum of Natural History (abbreviated YPM, and where detailed locality information may be obtained) and in the collections of the Springfield Science Museum (abbreviated SSM). YPM numbers are six digits and refer to individual specimens; SSM numbers are fractional, include a hyphenated denominator, and refer to the slabs on which the specimens are preserved.

3.1 Mitchellichnus cf. *ferrydenensis* (Figs. 3A-B, number 3)

3.1.1 Genus

Mitchellichnus Walker, 1985

3.1.2 Type ichnospecies

Mitchellichnus ferrydenensis Walker, 1985.

3.1.3 Material

One specimen, YPM 227941.

3.1.4 Description

A single short (2.5 cm long) trackway segment preserved as a convex hyporelief, composed of two track rows, between which are three parallel medial impressions. The external and internal widths of the trackway are 6.4 and 3.0 mm, respectively. Individual tracks are simple circular punctate marks up to 0.3 mm wide on the left side of the trackway, and elongate and dash- to teardrop-shaped marks having a maximum length of 0.8 mm on the right side of the trackway. Within rows, the tracks are arranged linearly to triangularly into series that have a stride of 1.9 to 2.7 mm. The series have a maximum of three tracks, exhibit staggered to opposite symmetry, and are variable in their orientation relative the trackway midline, with angles measuring from 55 to 88°. The central medial impression is deepest and measures about 0.3 mm wide, whereas the two lateral ones are each between 0.1 and 0.2 mm wide.

3.1.5 Remarks

Walker (1985) erected *Mitchellichnus* for material collected by Rev. Hugh Mitchell from Montrose, Scotland in 1859. The taxon is similar to *Paleohelcura* and *Stiaria*, but can be distinguished from these ichnogenera by having three parallel medial impressions and two extra series of six imprints that are oriented obliquely to the trackway's main axis. Although included in the diagnosis, Walker (1985) noted that the paired oblique series of appendage marks are not always present, such that some specimens consisted of two rows of tracks arranged into series of threes, between which are only the three medial impressions.

YPM 227941 is most similar to *M. ferrydenensis* specimens lacking the paired series of six imprints. However, it differs from the type specimens, which have a maximum width of 70.0 mm, in being much smaller. Although size is not typically regarded as a valid criterion for

distinguishing ichnotaxa (Buatois and Mángano, 2011, p. 28), discrete size classes separated by an order of magnitude are an exception to this rule (Minter and Braddy, 2006b). Therefore, if additional trackways similar in size to the Plainville specimen are found, without intermediates, the small trackways may warrant the recognition of a new ichnospecies, assuming that *Mitchellichnus* is retained as a separate ichnogenus (see discussion below).

3.1.6 Discussion

Fillmore et al. (2012) assigned a Mississippian-aged trackway from the Mauch Chunk Formation with a triple-medial impression to the ichnogenus *Stiaria*; however, this specimen is better assigned to *Mitchellichnus*, along with the Plainville specimen. The Mauch Chunk and Plainville occurrences of *Mitchellichnus* are the first outside of the type locality, and also the first specimens that can be attributed to a trace maker (Walker was unsure of the trace maker for her specimens, which are too large to have been made by archaeognathans).

3.2 Siskemia elegans (Figs. 3A-B, number 1)

3.2.1 Genus

Siskemia Smith, 1909

3.2.2 Type ichnospecies

Siskemia elegans Smith, 1909.

3.2.3 Material

One specimen, YPM 227939.

3.2.4 Description

A single short (3.6 cm long) trackway segment preserved as a convex hyporelief, composed of two rows of grouped tracks between which are two parallel medial impressions. The external and internal widths of the trackway are 7.4 and 2.8 mm, respectively. Individual tracks are elongate and crescentic- or teardrop-shaped, with a maximum length of 2.6 mm; in many cases the tracks converge proximally so as to resemble a single, trifid impression. Tracks are arranged linearly within series that have a stride of 2.6 to 3.6 mm. Series exhibit staggered to alternate symmetry and are variable in their orientation relative to the trackway midline, with angles measuring from 52 to 97°. The two medial impressions, which are about 0.4 mm apart, are offset slightly to the right side of the trackway, are continuous, have equal thickness (~0.3 mm), and are about the same depth.

3.2.5 Remarks

Siskemia was erected by Smith (1909) and was revised by Pollard and Walker (1984) and Walker (1985), who provided a detailed diagnosis of this and other of Smith's taxa. Among the morphological characteristics that Walker (1985) considered diagnostic of *Siskemia* were two parallel rows of grouped appendage imprints, between which were two parallel medial impressions. YPM 227939, with a double medial impression and parallel rows of grouped tracks, fits this diagnosis and is therefore assigned to *Siskemia*.

Of Smith's (1909) seven *Siskemia* ichnospecies, Walker (1985) considered only three ichnospecies to be valid, *S. bipediculus*, *S. elegans*, and *S. lata-via*. YPM 227939 is much smaller than both *S. bipediculus* and *S. lata-via*, and it also has a more regular track pattern than is seen in *S. lata-via*. Instead, YPM 227939 is similar in size and overall trackway morphology to *S. elegans* and is therefore assigned to that species.

It is noteworthy that, in addition to the double medial impression typical of all *Siskemia* ichnospecies, some *S. elegans* also exhibit an intermittent third impression (Walker 1985). However, the three medial impressions of *S. elegans* are different from those of *M. ferrydenensis* described above in that the lateral medial impressions are thicker than the central one and are continuous, whereas in *M. ferrydenensis* the central medial impression is thicker and occurs more regularly.

3.2.6 Discussion

Buatois et al. (1998) described a Pennsylvanian-aged trackway from the Tonganoxie Sandstone of Kansas with a double-medial impression along part of its length and assigned it to the ichnogenus *Stiaria*, arguing that the double-medial drags were too poorly defined and narrowly separated to warrant assignment to *Siskemia*. However, the medial drags are clearly visible in their figures, and the diagnosis of *Siskemia* does not indicate that the drags must be widely spaced. Indeed, the Plainville *Siskemia* also has closely spaced medial drags. The Kansas specimen could be considered a compound trace fossil composed of both *Stiaria intermedia* for those portions with a single drag, and *Siskemia elegans* for portions with a double drag (Pickerill, 1994).

3.3 Stiallia pilosa (Figs. 3G-J)

3.3.1 Genus

Stiallia Smith, 1909

3.3.2 Type ichnospecies

Stiallia pilosa Smith, 1909

3.3.3 Material

Two specimens, YPM 236965 and 237004.

3.3.4 Description

YPM 236965 is a short (1.6 cm long), gently curving trackway segment preserved in convex hyporelief and consisting of two elements: two rows of multiple furrows oriented at an oblique angle to the long axis of the trace, and a single medial impression. The trackway has a maximum width of 7.4 mm and an internal width between 1.5 and 3.2 mm. Individual furrows, which are elongate and ovate, teardrop-shaped, or wavy in outline, vary in length from 1.0-3.0 mm, and measure 0.1 to 0.6 mm wide. The furrows are oriented 56 to 90º to the trackway midline. The repeat distance, or stride, between furrows is 0.4 to 2.1 mm. The medial impression is continuous and is 0.5 mm wide.

YPM 237004 is a 6.6 cm long gently curving trackway preserved as a convex hyporelief. It is composed of three elements: a single row of overlapping furrows, a long but discontinuous impression measuring 0.2 to 0.4 mm wide, and short, thin (~ 0.1 mm wide), arcuate impressions that appear mid-length along the trackway. The furrows, which measure from 0.7 to 3.1 mm long and up to 0.4 mm wide, are straight and dash-like to slightly pinched and teardrop-shaped. They are oriented obliquely to nearly parallel with the trackway midline, and in some places are arranged into groups of up to three. The trackway has a maximum width of 7.9 cm.

3.3.5 Remarks

The ichnogenus *Stiallia* is composed of two rows of multiple overlapping furrows, between which an axial mark may be present (Walker, 1985). Five ichnospecies were originally described, but based on intergrading morphologies, Pollard and Walker (1984) and Walker (1985) synonymized them with *S. pilosa*. These authors referred another of Smith's ichnospecies, *Carrickia berriana*, to *Stiallia* as *S. berriana*. YPM 236965 lacks the regularly spaced, circular to lunate medial impressions characteristic of *S. berriana* and we assign it to *S. pilosa* instead. YPM 236965 resembles *S. pilosa* from the Tonganoxie Sandstone of Kansas (Buatois et al. 1998, fig. 7), but the individual furrows are oriented at a greater angle relative to the trackway midline so that there is less overlap between the furrows than in the Kansas specimens. YPM 237004 has only one set of furrows and is only tentatively referred to this taxon.

3.3.6 Discussion

Stiallia has been interpreted as an arthropod locomotion trace (Smith, 1909; Walker, 1985), a feeding trace (Minter and Braddy, 2009), and a combined feeding and locomotion trace (Buatois et al., 1998). The last authors have described this taxon in association with *Tonganoxichnus buildexensis*, and based on this association, as well as similarities in size, suggested that their examples were produced by archaeognathans. Traces similar to those described by Buatois et al. (1998) have been produced by recent archaeognathans under experimental conditions (see below) when they attempt to free themselves from being mired in a wet substrate. Our observations confirm that archaeognathans make *Stiallia*-like traces. They also suggest that at least some fossil examples, particularly those attributed to archaeognathans, may be a combined escape and locomotion trace.

3.4 Stiaria intermedia (Figs. 3A-D, numbers 2 and 4-8; Figs. 3E-F)

3.4.1 Genus

Stiaria Smith, 1909

3.4.2 Type ichnospecies

Stiaria quadripedia Smith, 1909.

3.4.3 Material

Seven specimens, YPM 227940, 227942-227946, and 236963.

3.4.4 Description

Short (up to 4.9 cm long), straight to tightly curving trackway segments preserved as concave epireliefs and convex hyporeliefs, composed of two rows of tracks, with or without a single medial impression. The external widths of the trackways vary among specimens from 5.1 to 7.1 mm; internal widths are between 2.1 and 3.7 mm. Individual tracks are either simple circular punctate structures between 0.3 and 0.8 mm wide, or elongate and straight, crescentic, or teardrop-shaped, with a maximum length of 1.9 mm. Within rows, tracks are typically arranged linearly or triangularly into series that have a stride of 1.9 to 5.2 mm, although in one example (Fig. 3E-F) the series are more difficult to discern. The series consist of up to three tracks, are arranged in staggered to opposite symmetry, and are variable in their orientation relative the trackway midline, with angles measuring from 32 to 86°. The tapering of tracks in the direction of locomotion (Sadler, 1993) indicates that in these fossils linear series are staggered forward, rather than backwards. Where a medial impression is present, it is typically of uniform thickness (0.1-0.2 mm), although one exhibits pinching and swelling. One

trackway, YPM 227944, exhibits a short (≥ 5% of the trackway length) secondary medial impression that parallels the main one.

3.4.5 Remarks

Stiaria, another of Smith's (1909) taxa, was also revised by Pollard and Walker (1984) and Walker (1985). Minter and Braddy (2009) have provided an extensive synonymy of similar taxa, but a remaining point of contention is whether or not *Paleohelcura* Gilmore (1926) should be considered a junior synonym. *Stiaria* consists of series of two to four tracks arranged into two rows, between which may lay a medial impression. Two species are currently recognized as valid, *S. intermedia* and *S. quadripedia*. *S. intermedia* is smaller (≤ 18-20 mm track width) and has up to three tracks per set, whereas *S. quadripedia* is larger and has up to four tracks per set. Trackways YPM 227940, 227942, 227943, and 227946 are unequivocally assignable to *Stiaria intermedia* based on size and maximum of three tracks per set. The second medial impression in 227944 is a minor trackway feature, and we thus consider it to be minor morphological variant of typical *S. intermedia* morphology (sensu Minter et al., 2007).

3.5 Tonganoxichnus buildexensis (Fig. 4)

3.5.1 Genus

Tonganoxichnus Mángano, Buatois, Maples, and Lanier, 1997

3.5.2 Type ichnospecies

Tonganoxichnus buildexensis Mángano, Buatois, Maples, and Lanier, 1997.

3.5.3 Material

Thirteen specimens, SSM 2007/6-40, 2011/9-1, 2012/4-1, 2012/4-2, 2012/4-3, YPM 227991-227992 and 236967-236972.

3.5.4 Description

Bilaterally symmetrical traces that consist of three longitudinally differentiated regions (here termed anterior, central, and posterior). The maximum length of these traces is 16.2 mm (or 15.0 mm without the anterior parallel furrows). Individual traces vary widely in length and completeness due to a variety of factors, including variations in size and posture of the animals, as well as substrate consistency.

The anterior region consists of a maximum of two elements. At the front are one or two furrows (labeled m in Fig. 4), measuring up to 2.6 mm long, on opposite sides of and elongate in the direction of the trace's longitudinal axis. Posterior to the furrows an ovate, rectangular, or irregularly shaped depression (labeled h) measuring 1.1 to 2.4 mm long may be present.

The central region (labeled tl) of the trace also consists of up to two elements. Medially, a maximum of three pairs of circular, ovate, or irregularly shaped depressions (labeled from anterior to posterior as tl1- tl3) are arranged in two rows on opposite sides of the trace's longitudinal axis. Individual depressions are sometimes subdivided into two sections (labeled c+tr in Fig. 4D) by a thin ridge of sediment. The anterior pair of these depressions is oriented anteriorly to anterolaterally (between 23 and 83°), the central pair is oriented anterolaterally to laterally (between 57 and 120°), and the posterior pair is oriented laterally to posterolaterally (between 92 and 157°). A few specimens exhibit additional ovate to teardrop-shaped depressions (labeled t) measuring 0.4 to 0.5 mm long, lateral to the paired medial

depressions. These lateral depressions are inferred to be part of the overall trace because their long axes are parallel to and in line with the long axes of the nearby medial depressions, and because a thin ridge in one example (Fig. 4F, tl3) connects the medial and lateral depressions.

The posterior region of the trace (labeled a) consists of a rectangular or ovate depression, which may be subdivided into two or more rectangular subsections in well-preserved examples, and a series of paired elongate furrows. The subsections of the depression are between 0.7 to 1.7 mm long. The furrows (labeled s) originate anteromedially within subsections of the depression and are oriented posterolaterally, between 149 and 174° relative to the trace axis. Each pair of furrows forms a chevron-like arrangement with an apical angle of 21 to 52°. When preservation is incomplete, furrows may occur without a depression (e.g., the posterior of impression 2 in Figs. 4A-B) or the depression may lack furrows (e.g., Figs. 4E-F).

3.5.5 Remarks

Currently, four ichnospecies of *Tonganoxichnus* are recognized. The more complete Plainville specimens are similar to *T. buildexensis*, the taxon to which we assign them, but they lack an elongate furrow (called a cylindrical projection in Mángano et al., 1997) at the posterior end of the trace. However, the absence of this furrow in Plainville specimens is most likely an artifact of tracemaker posture, and as such does not constitute an important difference. The Plainville specimens differ from other *Tonganoxichnus* species in lacking the L- to V-shaped leg imprints of *T. apacheensis* (Braddy and Briggs 2002; Minter and Braddy 2009), the fan-like array of maxillary palp scratches of *T. ottawaensis* (Mángano et al., 1997), and the repeated series of jumping impressions typical of *T. robledoensis* (Minter and Braddy, 2006a). Finally,

they differ from specimens described by Benner et al. (2011) in having ventromedial, rather than ventrolateral, stylus imprints.

3.5.6 Discussion

The origins of the various elements of these traces have been discussed in depth elsewhere (e.g., Mángano et al., 1997, 2001; Braddy and Briggs, 2002; Minter and Braddy, 2006a) and, accordingly, are only briefly summarized here. Anteriorly, the two elongate furrows are interpreted as having been made by the maxillary palps, and the central oval region by the ventral surface of the head. In the central region, the medial ovate structures are thought to have been produced by the proximal portions of the insect's legs (i.e., the coxae and trochanters), whereas the lateral impressions are thought to be produced by the distal tarsal elements. Posteriorly, the segmented abdomen produced a large ovate impression and the abdominal styli left the chevron-shaped pairs of furrows. These interpretations are supported by observations of experimentally produced body imprints of extant archaeognathans (Sturm, 1955; this study).

3. Experimental Methodology

The trackways with double- and triple-medial impressions associated with archaeognathan trace fossils raise a number of questions. Were they also produced by archaeognathans? If so, what anatomical structures and behaviors result in the different trackway morphotypes? Why are single-medial impressions abundant, and double- and triple-medial impressions rare? How does sediment variation affect trackway morphology? We conducted neoichnological experiments with modern archaeognathans and with the morphologically similar silverfish (order Thysanura; Fig. 1D) to address these questions. Our

experiments with these insects compliment those by previous researchers (e.g., Sturm, 1955; Manton, 1977) in that previous studies only used unrealistic substrates, such as smoked paper in trace production, whereas we used both smoked glass and muddy substrates similar to those in which the fossils were made, to examine trace production. Further, our experiments are the first to consider how different numbers of medial impressions are made.

The insects used in this study were identified using Powell and Hogue (1979) and Wygodzinsky and Schmidt (1980). They included the bristletails *Mesomachilis* sp., collected from redwood stumps in Kneeland, California, *Pedetontus saltator*, from a quarry in Canaan, Connecticut, and *Trigoniophthalamus alternatus*, from rock outcrops in New Britain and Middletown, Connecticut. In addition to experiments conducted with bristletails, experiments were conducted with the silverfish *Thermobia domestica*, collected from Storrs, Connecticut, because thysanurans retain a body plan similar to that of archaeognathans (Fig. 1D), and because the fossil records of both groups overlap (Shear et al., 1984; Kukalova-Peck, 1987; Shear and Kukalova-Peck, 1990; Kluge, 1996).

Both *P. saltator* and *T. alternatus* are parthenogenic (Wygodzinsky and Schmidt, 1980) and thus all specimens collected were females. The sex of *Mesomachilis* specimens was not determined. *T. domestica* included both males and females. The length of the insects, measured from the maxillary palps to the tip of the terminal filament, was 18.9-23.5 mm for *Mesomachilis* sp., 11.1-13.3 mm for *P. saltator*, 20.5-23.0 mm for *T. domestica*, and 7.8-14.0 mm for *T. alternatus*. All insects weighed less than 0.1 g.

Archaeognathans have a primitive body plan with numerous appendages that that may leave traces during locomotion. Anteriorly, two large maxillary palps (Figs. 1A-C) are used for manipulating food, probing the substrate, and for climbing (Smith, 1970). Posteriorly, most

abdominal segments bear paired styli that support the abdomen (Figs. 1A-C). In extant species, enlarged styli on genital segments 8 and 9 are known as gonostyli. The caudal end of the abdomen bears a long, medial, tail-like terminal filament (Figs. 1A-C) that is struck against the ground to propel the insect during a jump—the motion for which the group gets its common name (Evans, 1975; Manton, 1977). In modern bristletails (but not in Monura), the terminal filament is flanked by lateral cerci (Fig. 1A-B) that may also strike the ground during a jump. Which of these body parts left traces during locomotion was determined from video recordings. Behaviors exhibited by the animals were broadly categorized as locomotion, which included walking or jumping, and resting, which was defined as remaining in the same place for five or more seconds. However, animals at "rest" were not always motionless, as antennae and/or maxillary palps often moved while animal remained in place.

Experiments were conducted on two media: smoked glass, which replicated the hard substrates on which many of the modern species were found, and wet mud, which replicated the sediment conditions in which the fossils were made. In glass experiments a plate was held above the flame of a butane lighter until it was lightly covered with soot. Once covered, the plate was allowed to cool, and then was placed in an enclosure with the test insects. In multiple trials, all four apterygote species were prompted to walk across the soot-covered glass by blocking alternate routes. Once an individual had walked across the plate, the resultant trackway was illuminated from below and photographed. (Unfortunately, video cameras were not available at the time these experiments were conducted.)

Trackways produced in muddy substrates were made by dropping the insects onto a mud-filled pan and allowing them to traverse the surface. Following trials in various substrates, experiments were carried out using mud collected from the quarry in which the

fossils were found because delicate arthropod trackways were observed on it in the field. The grain size for this sediment was mostly $\geq 4\phi$, with minor amounts that were $\leq 3.75\phi$. Thus, the sediment was silt or finer with a minor amount of very fine-grained sand (Nichols, 1999).

Mud mixtures were produced by filling an 11.1 x 5.2 x 0.6 cm clear plastic pan with dried, powdered sediment and then adding water. No manual compaction of the sediment occurred; rather, it was allowed to remain loose. The sediment was planed off to the top of the pan and then weighed on a scale to the nearest 0.1 g. Water was then added to the sediment with a dropper bottle until it was saturated. Upon saturation, the pan was weighed again to determine the water weight by subtraction. Initial sediment and water weights were 21-23 g and 17-19 g, respectively. Thus, the initial sediment-water mixtures were ~ 43-47% water by weight. Mixtures with higher water percentages were not used because water began to collect on the surface, which could have negatively affected trace production.

Before the experiments began, the saturated mixture was again planed off to produce a relatively smooth surface for track production. This procedure removed a small amount (typically 0.2 g) of the mixture, and the remaining amounts of water and sediment were calculated. During the experiments, smaller *T. alternatus* often did not produce a trace, especially in drier substrates. Consequently, larger individuals (> 5 mm body length) were used repeatedly. Individuals of the silverfish *T. domestica* were also used repeatedly.

In order to understand how desiccation affected trace production, two variables were recorded before each experimental trial: the time elapsed since the mixture was prepared, and the percent water composition of the sediment. Additional observational data included what

types of traces were produced at a specific time, how complete the traces were, and how pre-existing traces were affected as time elapsed.

4. Results

4.1 Jumping Bristletail Traces

4.1.1 Body Imprints

Thirty-five body imprints, measuring from 6.5 to 14.9 mm long and 1.8 to 3.9 mm wide, were made by *T. alternatus* in fine-grained mud experiments (Fig. 5). They were produced during the take-off and landing phases of jumping. Take-off traces (Figs. 5A-F) were about twice as common as landing traces (Figs. 5G-J) because they often overprinted and obliterated the preceding landing traces. Traces made upon landing were preserved when the bristletails walked or sidestepped before jumping. Commingling of the two trace types occurred when the animal took only a short lateral step before jumping, especially when the terminal filament became stuck (Figs. 5I-J).

Imprints were bilaterally symmetric and, like fossil specimens, were divisible longitudinally into different regions. All of the traces shared certain features, such as the presence of six imprints made by the distal tips of the thoracic legs. However, there were morphological differences between traces produced during take-off and landing. For example, anteriorly, take-off traces exhibited one or two elongate, straight to curved furrows oriented parallel or oblique to the midline of the trace, produced by the maxillary palps as they pushed into the substrate. By contrast, the anterior of landing traces only contained small circular or ovate structures produced by the palps as they gently touched the mud (Figs. 5G-H). Another

landing trace exhibited an ovate imprint produced by the ventral surface of the head. In both take-off and landing traces, the abdomen often, but not always, left a deep imprint that sometimes exhibited segmentation and that rarely contained chevron-shaped pairs of imprints made by the abdominal styli (Figs. 5A-B). Some abdomen imprints included fine-scale scratches produced by the styli as the animal moved away from the body imprint (Figs. 5I-J). Posterior to the abdomen imprint, take-off traces exhibited a long, thin imprint of the terminal filament that was made as this structure was struck against the mud (Fig. 5A-D). Additionally, take-off traces occasionally exhibited imprints of the lateral cerci to the side of terminal filament imprint. Landing traces did not always exhibit a terminal-filament imprint because this structure was sometimes held above the substrate, and they never exhibited imprints of the lateral cerci. In addition to differences resulting from animal behavior, sediment saturation also caused variation in trace morphology. For example, in firm substrates, only the distalmost parts of the palps, legs, and terminal filament impressed the mud (Fig. 5E-F).

4.1.2 Trackways

Mesomachilis sp., *P. saltator*, and *T. alternatus* were used to make eleven trackways on smoked glass and *P. saltator*, and *T. alternatus* made 22 trackways in mud (Fig. 6). The trackways measured between 2.2 and 7.7 mm wide and consisted of two rows of tracks between which varying numbers of medial impressions occurred. Tracks were circular, ovate, or elongate, and sometimes exhibited drag marks tapering in the direction of locomotion. Within each row the tracks were typically, but not always, arranged linearly or triangularly into series of up to three tracks. When track series were present, they exhibited alternate or opposite symmetry. The series were typically oriented obliquely forward, although some were oriented

obliquely backward, and had angles relative to the trackway midline from 12 to 175º. Stride length ranged from 1.1 to 6.2 mm and varied depending on the size of the individual, as well as its speed and the ease with which it traversed the substrate. In some cases, such as when the animal was climbing onto the smoked glass plate, or when the animal became mired in the mud (Figs. 6F-G), the legs were raked across the substrate, producing elongate scratch marks rather than simple circular tracks. In smoked-glass experiments tracks often consisted of two smaller imprints left by the tarsal claws, but this level of detail was not seen in mud experiments. As noted above, trackways typically began with a landing trace, and they either ended with a jumping trace, or abruptly where the animal climbed out of the pan.

The terminal filament, lateral cerci, and abdominal styli all produced medial impressions between the track rows. In one case, an antenna produced an impression after it contacted and became stuck in the mud, but its position relative to the track rows is unknown because no tracks were produced in the resultant trace.

The number and arrangement of the medial impressions was dependent on sediment saturation and its affect on the posture and behavior of the animal after it landed. In wet, sticky substrates the inertia of the landing caused the terminal filament to impact and adhere to the substrate (Fig. 6A). Many test animals attempted to free the filament by jerking the abdomen upward, but most were unsuccessful. The terminal filament was pulled through the mud as the animal walked away from the landing site, producing a medial impression, about 0.1-0.2 mm wide, between the two rows of tracks (Figs. 6B-C). At irregular intervals, the impression of the styli and/or lateral cerci produced additional, fainter impressions lateral to the one produced by the terminal filament (Figs. 6D-G). In this way, two, three, or more medial impressions sometimes resulted. Triple medial impressions were produced twice, but in

slightly different ways. The terminal filament produced a thick central impression in both cases, but the two lateral impressions were made by styli in one trackway (Fig. 6D-E) and by cerci in the other (Fig. 6F-G).

In non-cohesive media (and rarely when the terminal filament was dislodged from the mud, see below), the terminal filament was held above the ground so it left no trace (Fig. 6H). The skid-like abdominal styli produced two rows of medial impressions that, depending on the size of the individual, were from 0.2 to 1.1 mm apart (Sturm 1955, fig. 5; Figs. 6I-N). Gonostyli impressions were more closely spaced than those of the anterior styli (Figs. 6I-L) due to the distal tapering of the abdomen. Slight variations in the insects' posture and behavior resulted in anterior or posterior styli leaving more pronounced impressions. For example, thick, continuous, and closely spaced gonostyli impressions were made when the abdomen was held horizontally in smoked glass experiments; these marks were flanked laterally by fainter impressions of variable length produced by the anterior styli (Figs. 6I-J). By contrast, in a mud experiment the anterior styli remained in contact with the substrate and made widely spaced, continuous impressions, whereas gonostyli left narrowly spaced, tick-like impressions as the posterior abdomen was jerked up and down (Figs. 6K-L). As the substrate dried, styli impressions became fainter and more intermittent (Figs. 6M-N), until they disappeared altogether.

During three experiments a bristletail was able to free its terminal filament from the mud after having dragged it. This change in posture resulted in different arrangements of medial impressions along segments of each trackways' length. For example, a medial impression produced by the terminal filament is seen behind and to the right of the landing trace in Figs. 5E-F. The impression was made when the filament was allowed to contact the

substrate as the animal began to walk, and is flanked on both sides at irregular intervals by fainter impressions made by the styli, such that there are at different places one, three, six, or seven medial impressions. (A maximum of three are visible in the part of the trackway visible in the photograph). After walking a short distance, the terminal filament was pulled out of the substrate by repeated upward jerking of the abdomen, and the trackway subsequently exhibited only the two rows of impressions made by the styli (Figs. 6K-L). The animal repeated the behavior of allowing the filament to touch the substrate and then pulling it out, thereby producing two more trackway segments with single and double medial impressions.

4.2 Silverfish

4.2.1 Trackways

Eleven trackways were produced by *T. domestica* on smoked glass and 23 were made in wet mud (Fig. 7). The trackways measured between 4.5 and 9.7 mm wide and consisted of two rows of tracks between which medial impressions often occurred. The tracks were typically circular, triangular, or ovate in shape. As with the bristletails, tracks on smoked glass often exhibited two marks left by the tarsal claws (Figs. 7A-B). In mud experiments, the tracks sometimes exhibited drags tapering forward in the direction of locomotion (Figs. 7C-D), and in one experiment the tracks merged together into large, sinuous to irregularly shaped depressions (Figs. 7G-H). Within the rows, tracks were usually arranged into series (e.g., 7A-D), although series were not produced in some mud experiments when the animal struggled to cross the substrate (e.g., left side [up] of trackway in Figs. 7E-F). Where series were present, they exhibited staggered to alternate symmetry, had a maximum of three tracks each, and were arranged linearly or triangularly. Series were usually oriented forward but occasionally were

oriented backward, and angles relative to the midline ranged from as low as 23 to as high as 163º. Stride lengths measured between 1.8 and 7.1 mm, and were generally larger in non-cohesive substrates.

Various structures, including antennae, gonostyli, lateral cerci, and the terminal filament produced medial impressions under different conditions. As with the bristletails, the saturation and cohesiveness of the substrate, as well as the insects' reaction to these factors, affected the presence and arrangement of impressions. For example, the lateral cerci and antennae only produced impressions in wet mud when they touched, and then became stuck to, the substrate (e.g., Figs. 7E-F).

In smoked-glass experiments, all of the trackways exhibited a central impression produced by the terminal filament (Figs. 7A-B). In three of the trackways the filament impression was flanked by short impressions made by the gonostyli, producing double impressions when one gonostylus impressed, and three when both were involved.

In mud experiments, the silverfish responded by elevating their bodies to decrease contact with the wet substrate. This behavior resulted in 12 trackways that lacked a medial impression (e.g., Figs. 7C-D). However, the insect's antennae sometimes got stuck, and in six experiments one or both left thin impressions that were, with one exception, offset to one side of the trackway (e.g., Figs. 7E-F). The terminal filament left an impression in nine trackways (e.g., Figs. 7G-L), and in all but one the impression was flanked by those made by different structures. Lateral cerci left impressions in four trackways, three of which were made by the same fatigued animal (e.g., Figs. 7I-L). This individual produced three trackways with a double-medial impression when the left lateral cercus and terminal filament dragged (e.g., Figs.

7I-J). In all three, the mark made by the cercus was thinner than that of the terminal filament. This insect also made a triple-medial impression when the terminal filament and both cerci scored the substrate (Figs. 7K-L). As in the smoked-glass trials, the gonostyli only produced short drag segments (e.g., Figs. 7K-L).

4.3 Role of Sediment Saturation in Trace Production and Preservation

The results of our experiments are in agreement with those of other researchers (e.g., Davis et al., 2007; Falkingham et al., 2011), and show that there was an optimal window of sediment saturation conditions outside which trace production and preservation was negatively impacted (Fig. 8). At higher saturation levels (i.e., ≥ 45% water by weight), traces were often reduced over time to their deepest components as a result of sediment flow. These losses mimic those resulting from undertrack fallout (Goldring and Seilacher, 1971). For body traces, deep imprints made by the maxillary palps, abdomen, and terminal filament were more likely to be preserved, whereas leg, styli, and lateral cercus imprints were more likely to be destroyed. Similarly, trackways lost shallower tracks and fainter medial impressions, such that only the terminal filament impression remained. At lower saturation levels (i.e., below ≤ 36-38%) trace production decreased due to the failure of the insects to penetrate the firmer substrate. Those traces that were produced in drier substrates were more sharply defined than those in wetter sediments, and they retained their shape better as water evaporated.

5. Discussion

5.1 Identity of the Fossil Trace Makers

5.1.1 Body Imprints

As noted above, *Tonganoxichnus* is typically attributed to the Archaeognatha, although there has been some dissent. For example, Rasnitsyn (1999) used three main points to argue against attributing *Tonganoxichnus* to the Archaeognatha. If he were right, the fossil record of archaeognathans would be restricted to body fossils and *Tonganoxichnus* must have been produced by some other, as yet unidentified, group of insects. However, as we outline here, evidence from experimentally produced traces, as well as from the fossils themselves, indicate that archaeognathans are the likely producers of *Tonganoxichnus*.

First, Rasnitsyn (1999) noted that the leg imprints in *T. buildexensis* are near the midline of the trace, which suggested that proximal leg segments (coxae and trochanters) made them. By contrast, he expected the distal tarsus to impress during jumping. However, *T. buildexensis* exhibits tarsal imprints (Mángano et al., 2001; Figs. 4A-B, and E-F), and Sturm (1955, fig. 7) showed that the coxae of extant bristletails make imprints during jumping. Thus, fossils with coxae imprints are not evidence against an archaeognathan producer.

Second, Rasnitsyn suggested that the fossil trace maker's terminal filament attached to abdominal segment eight, instead of segment ten, as in archaeognathans. This interpretation was based on the assumption that the terminal filament made two separate (anterior and posterior) imprints. The posterior imprint is separated from the rest of the fossil and is long and thin. In modern jumping traces, identical imprints are made by the terminal filament (Fig. 5), suggesting that this organ made the posterior imprints in the fossils. However, an ovipositor may have made the anterior imprint (Mángano et al., 1997, 2001; Minter and Braddy, 2006a). This alternative hypothesis could only be falsified if a fossil was found with both imprints connected. Without such a fossil, it is impossible to know if the same, or different, organs made the two imprints.

Third, Rasnitsyn argued that partial terminal filament impressions indicated that the trace maker's jumping behavior was different from that of archaeognathans, which he predicted should leave deep, continuous marks. However, bristletails don't always use the terminal filament in jumping (Evans, 1975), and in those cases it is unlikely to leave a trace. Further, the terminal filament did not completely impress in many of our experimentally produced jumping traces (e.g., Figs. 5A-B and 5E-F). Finally, this argument presupposes that the fossils all exhibit jumping behavior, but landing also produces traces that often lack a filament imprint (e.g., Figs. 5G-H). Considering that many of the fossils resemble the modern landing traces, it is likely that some of the fossils lacking filament imprints were produced during landing. Thus, partial terminal filament imprints do not represent evidence against an archaeognathan trace maker.

Taken together, Rasnitsyn's (1999) arguments are unconvincing. To the contrary, the evidence for jumping, and the synapomorphy of elongate maxillary palps, argue strongly in favor of attributing *Tonganoxichnus* to the Archaeognatha.

5.1.2 Trackways

Experimental evidence presented here shows that the same species of track maker could have produced the three different, taxonomically recognized, medial impression morphologies seen in the Plainville fossil trackways, and that silverfish and jumping bristletail trackways are very similar. Thus, both groups must be considered when attempting to identify fossil track makers. Archaeognathan trackways can be differentiated from those of silverfish when they are associated with jumping or landing traces, since thysanurans cannot jump, and when the trackway exhibits oppositely symmetric track series, since silverfish are incapable of the gait

that produces symmetric traces (Manton, 1977). None of the Plainville trackways begin or end with a jumping or landing trace, but those exhibiting opposite symmetry (i.e., Figs. 3A-B, numbers 2, 3 and 7) can be attributed with certainty to archaeognathans. The other trackways (i.e., Figs. 3A-B, numbers 2, 6, 8), which have alternate symmetry, could have been made by jumping bristletails or silverfish. However, given that no definitive fossils of the latter group have been found in the Narragansett Basin, an archaeognathan affinity is more likely.

5.2 Production of the Medial Impressions in the Fossil Trackways

Our experimental results allow us to infer which structures were involved in the production of each medial impression arrangement in archaeognathan trace fossils. For example, the single medial impressions seen in the majority of *Stiaria intermedia* are likely result from the dragging of the terminal filament, whereas the thick central medial impression flanked by two fainter impressions, as seen in the Plainville and Mauch Chunk *Mitchellichnus ferrydenensis*, likely resulted from the terminal filament and either a pair of styli or the lateral cerci. (If the maker were a monuran, the styli must have made the lateral impressions since cerci are absent.) Finally, the double medial impressions seen in *Siskemia elegans* from Plainville and from the Pennsylvanian of Kansas likely resulted from the dragging of a pair of abdominal styli. The close spacing of the double impressions suggests that they were produced by a posterior pair of styli, possibly the gonostyli.

5.3 Relative Proportion of Fossil Trackway Morphotypes

As noted previously, most fossil trackways attributed to archaeognathans that have medial impressions have only one. This is at odds with our observation of modern bristletails

in the field and in the lab holding their terminal filaments above the ground, which would suggest that styli-produced double-medial impressions should be more numerous in the fossil record. Indeed, the fact that all of the smoked-glass experiments produced trackways with two rows of medial impressions supported this prediction.

However, the cohesiveness of muddy substrates, coupled with the inertia generated upon landing, caused the relatively large terminal filament to become stuck and drag through the mud as the animal walked. The smaller styli and lateral cerci produced fainter impressions that often did not survive, except under ideal conditions. Thus, the overwhelming number of single medial impressions in the fossil record results in part from the jumping—or, rather, landing—behavior of the animals in the wet sediments that preserve the traces.

5.4 New Interpretations of Stiallia and Tonganoxichnus

Our experimental results allow us refine our understanding regarding the production and preservation of archaeognathan trace fossils. For example, *Stiallia pilosa* is typically considered a feeding trace wherein the animal scratched the sediment while gathering food (Buatios et al., 1998). Our results, however, show that archaeognathans made *Stiallia*-like traces when they struggled to walk in soft, sticky mud to which their terminal filament adhered (Figs. 6F-G). The animals raked the mud with their legs, producing scratch marks that became closer together as they became increasingly mired. These experimental traces suggest that, in some cases, *S. pilosa* may be a combined locomotion and escape trace, rather than a feeding trace. This alternative interpretation is supported by observations from the fossils, some of which begin abruptly and exhibit prominent medial impressions (e.g., Buatois et al., 1998, figs. 7.3 and 14.2), suggesting that upon landing the animals dragged their terminal filaments.

Jumping traces produced by the bristletail *Trigoniophthalamus alternatus* most closely resemble the fossil *Tonganoxichnus robledoensis*, and support the interpretation that this ichnospecies represents jumping behavior (Braddy and Briggs, 2002; Minter and Braddy, 2006). By contrast, *T. buildexensis* has been interpreted to represent resting behavior, and *T. ottawensis* to represent feeding or defensive behaviors (Mángano et al., 1997; Buatois and Mángano, 2011). However, *T. buildexensis* exhibits considerable morphological variability that likely represents subtly different behaviors, such as jumping and landing. Indeed, Mángano et al. (2001) argued that some *T. buildexensis* were in fact landing traces. Our experimental results suggest that *T. buildexensis* with prominent maxillary palp and terminal filament imprints are jumping traces, whereas those lacking (or exhibiting fainter) imprints are possibly landing traces.

Mángano et al. (1997) also argued that floating animals made incomplete *T. buildexensis* exhibiting only maxillary palp and terminal filament imprints. Later authors have repeated this interpretation, while also suggesting undertracking as an explanation (Lucas et al., 2005a, b, Minter and Braddy, 2006). However, floating archaeognathans are unlikely given that these insects show no aquatic adaptations (Bechly and Stockar, 2011). Our results show that, in addition to undertracking, such partial body imprints may occur in two different sedimentary regimes. First, in wetter substrates, body imprints sometimes lost shallower portions of the trace due to sediment flow, and second, in firmer substrates, often only the palps and filament struck the substrate with enough force to leave an imprint (Fig. 5E-F). Thus, the presence or absence of thoracic and abdominal marks results from substrate variability in subaerial environments, not from floating or swimming behavior.

As noted above, *T. ottawensis* is generally regarded as a feeding trace, and the radial arrangement of partial impressions suggested to Mángano et al. (1997) that the archaeognathan producer engaged in lateral jumping. Although we cannot falsify the possibility of lateral jumps, such behavior was not seen in *Trigoniophthalamus alternatus*. Rather, this bristletail produced similar traces when the animal stepped sideways between landing and jumping, especially when the terminal filament became stuck (Figs. 5I-J). This suggests that sidestepping behavior may be responsible for the fossils. Furthermore, we question the interpretation that *T. ottawensis* represents feeding or defensive behavior. It is likely that *T. ottawensis* represents an archaeognathan that became stuck and used both its thoracic legs and palps to extricate itself. This alternative hypothesis is supported by the observation that the center of rotation in these traces is the terminal filament imprint, which suggests that this structure had become stuck. If this interpretation of is correct, then *T. ottawensis* is better interpreted, like *S. pilosa*, as a locomotion and escape trace.

5.5 Experimental Results and Implications for Ichnotaxonomy

Many researchers consider the ichnotaxonomy of arthropod trackways to be in a state of disarray, in part as a result of the use of non-standard criteria for erecting new taxa. Recently, there have been attempts to standardize the principles for defining new ichnotaxa, as well as for synonymizing existing taxa. For example, Minter et al. (2007) argued for the recognition of minor morphological variation within trace fossils, and suggested that it be regarded as insufficient for erecting new ichnotaxa or maintaining existing ones. They encourage others to synonymize ichnotaxa differentiated by only minor morphological variations when unequivocally intergrading fossil specimens are identified.

Our experimental work with bristletails and silverfish demonstrates that the number of medial impressions—historically used to define some ichnotaxa—varies due to minor behavioral differences among individuals, even within the same trackway. Thus, this character can be considered a minor morphological variation, which raises the question of whether the three ichnotaxa to which the Plainville trackways are attributed are best synonymized. The Plainville material does not contain intergrading specimens, but Buatois et al. (1998; fig. 7) described one specimen intergrading between a single and double medial impression, suggesting that synonymization may be warranted. For now, however, we defer synonymy pending the identification of additional intergrading material and a comprehensive review of the type specimens of the ichnogenera and their included species.

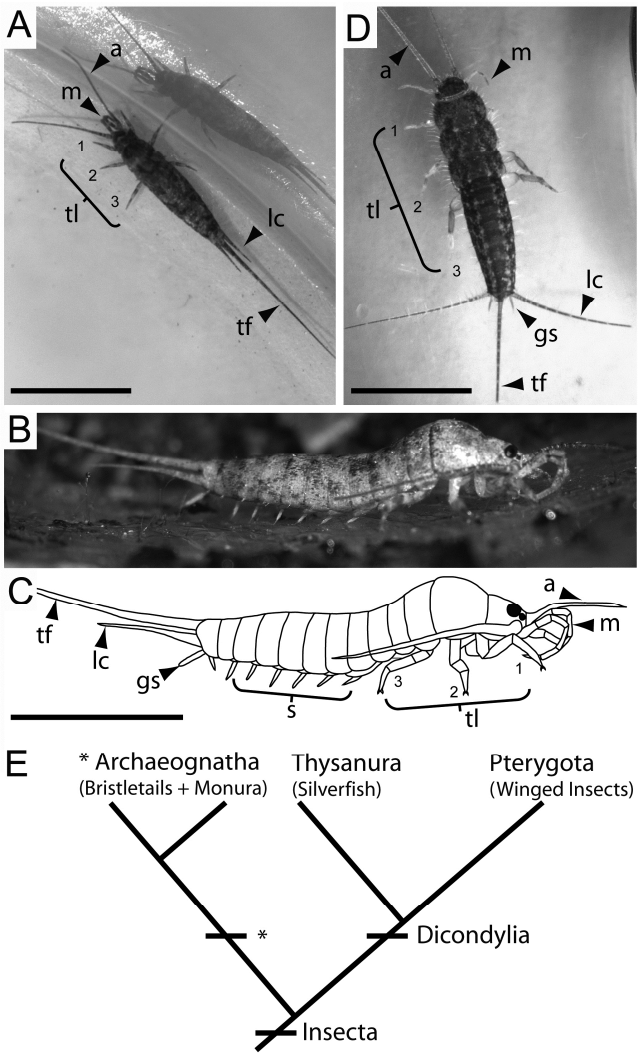
6. Conclusions

The body imprint *Tonganoxichnus buildexensis* and the trackways *Mitchellichnus ferrydenensis*, *Siskemia elegans*, and *Stiaria intermedia* are reported for the first time from the Pennsylvanian-aged Rhode Island Formation of the Narragansett Basin in Massachusetts. Experimental work with modern archaeognathans and thysanurans has provided insights into the trace makers, how the trackways were produced, the relative abundance of trackway morphotypes, and the behaviors exhibited by the traces. We regard the traces reported here as those of archaeognathans, and possibly just a single species, but the similarity of silverfish trackways to some of the fossils indicates that the latter group cannot be ruled out for alternately symmetric trackways. Regardless of trace maker, the single medial impression of *Stiaria intermedia* was likely produced by the animal's terminal filament, and the closely spaced double-medial impression of *Siskemia elegans* by the abdominal styli (probably the

gonostyli). The terminal filament and styli would have made the triple-medial impression of *M. ferrydenensis* if the maker were a monuran, or the terminal filament with either the styli or cerci if the trace maker was a machilid or thysanuran.

The morphology of archaeognathan trace fossils results from the combined effects of trace maker anatomy, behavior, and substrate interactions. Jumping in wet mud often causes the elongate terminal filament to become stuck, which affects the number of medial impressions, and when the animal becomes mired, the shapes of leg imprints. Only rarely do the smaller styli or cerci leave impressions lateral to the one made by the filament. If and when the medial filament is pulled up and out of the substrate—the typical walking position for extant archaeognathans—the abdominal styli leave faint paired impressions. Finally, our experimental work with extant jumping bristletails has helped to refine our understanding of the ichnogenera *Stiallia* and *Tonganoxichnus*, and emphasizes the importance of neoichnology in the study of trace fossils.

Figure 1. Insects discussed in this study and their relationships. (A) through (C) are archaeognathans, whereas (D) is a thysanuran. (A) *Pedetontus saltator* in dorsal view. (B) *Trigoniopthalamus alternatus* in lateral view. (C) Line drawing of the insect in (B). (D) *Thermobia domestica* in dorsal view. (E) A simplified cladogram showing the relationships of the Archaeognatha, Thysanura, and winged insects after Grimaldi and Engel (2005). Abbreviations: a = antenna; gs = gonostyli; s = (other) abdominal styli; tf = terminal filament; lc = lateral cercus; m = maxillary palps; tl 1-3 = thoracic legs one through three. Scale bars are 5 mm.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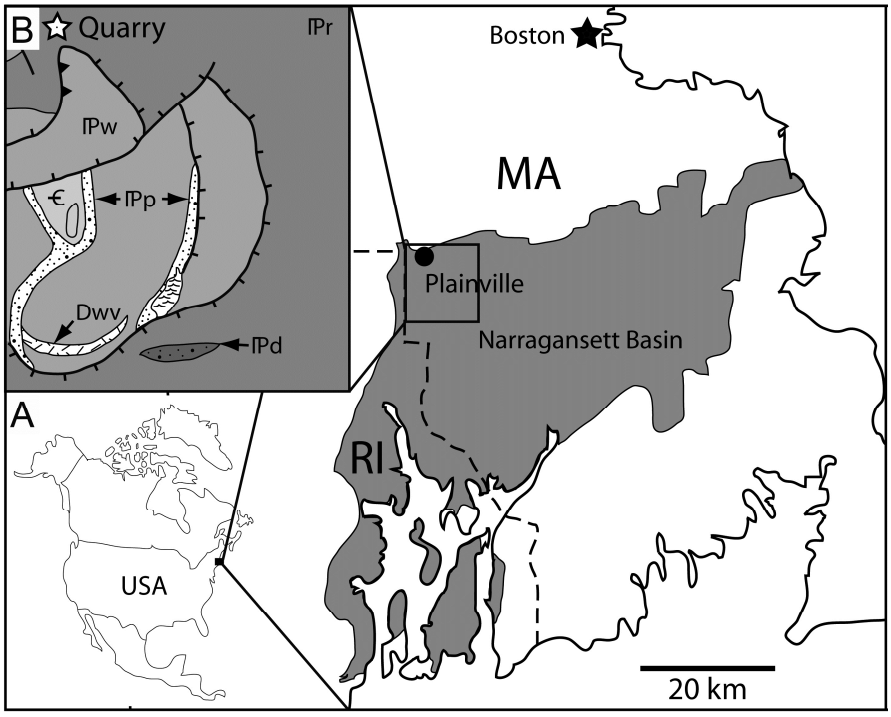
* Archaeognatha
(Bristletails + Monura)
Thysanura
(Silverfish)
Pterygota
(Winged Insects)
*
Dicondylia
Insecta

Figure 2. Geography and stratigraphy of the study area. (A) Map showing the location of southern New England and the Narragansett Basin. (B) Bedrock geology around Plainville, MA. Open star indicates the fossil locality. Map modified from Zen et al. (1983). (C) Simplified stratigraphic column of the basin showing the position of the fossil locality with an open star. Column modified from Skehan et al. (1979) with data from Maria and Hermes (2001) and Thompson and Hermes (2003). Abbreviations: MA = Massachusetts; RI = Rhode Island; Є =Cambrian inliers; Dwv = Wamsutta volcanics; PPd = Dighton Conglomerate; PPp = Pondville Conglomerate; PPr= Rhode Island Formation; PPw = Wamsutta Formation.


B
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Pp
Dwv
Pd
A
USA
Boston
MA
Plainville
Narragansett Basin
RI
20 km

Figure 3. Fossil insect trackways from Plainville, Massachusetts. (A) Photograph of a slab with five trackways, including one with a double (number one) and triple (number three) medial impression. (B) Interpretive drawing of (A). (C) Photograph of a slab with three trackways, including two (numbers 6 and 7) with short segments exhibiting double medial impressions. (D) Interpretive drawing of the slab in (C). Insets in (B) and (D) show close-ups of boxed areas with trackways on the main panels. Arrowheads indicate inferred direction of motion. (E) A tightly looping trackway. (F) Interpretive drawing of (E). (G) A trackway composed of two rows of scratches between which is a medial impression. (H) Interpretive drawing of (G). (I) An unusual trackway consisting of a single set of scratches, a long, continuous impression, and shorter, fainter impressions. (J) Interpretive drawing of (I). Trackways with single medial impressions are referred to *S. intermedia*, double impressions to *S. elegans*, and triple impressions to *M. ferrydenensis*. Scale bars are 1 cm.

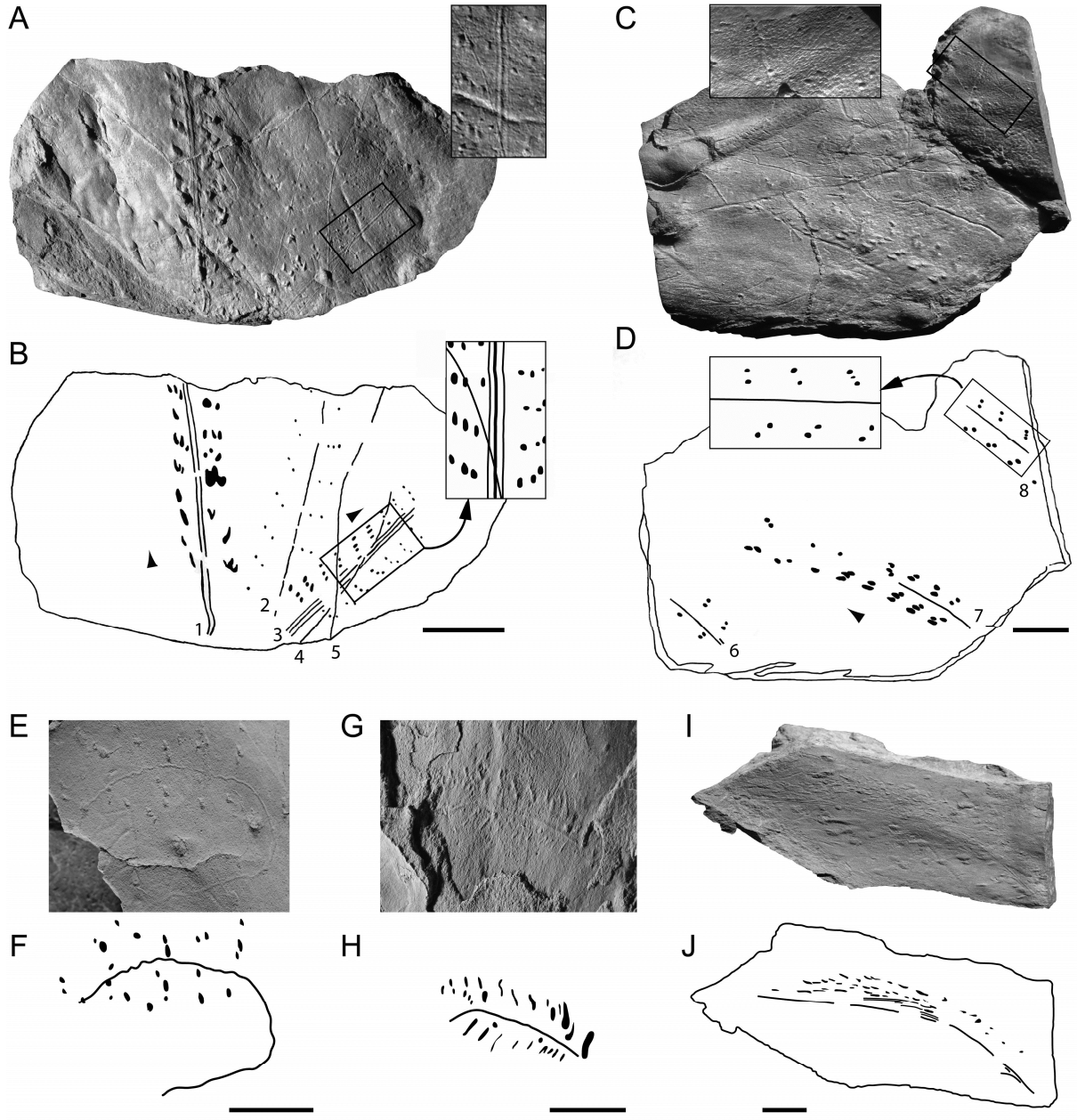
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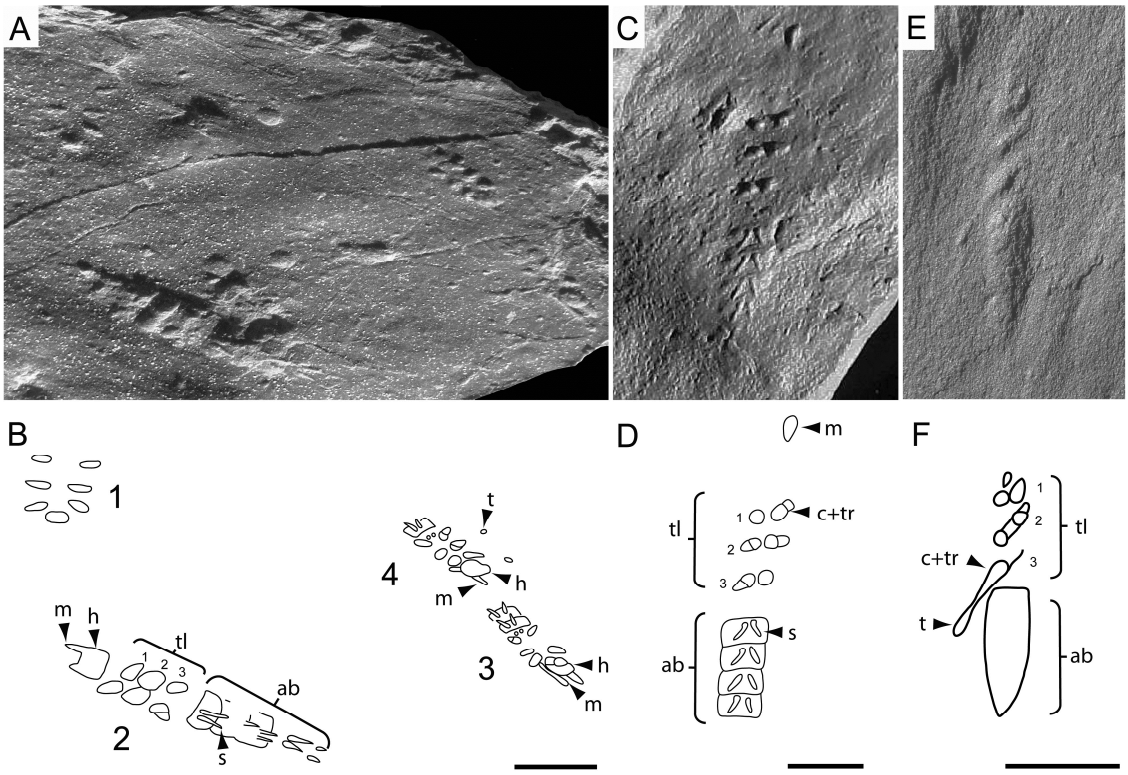
Figure 4. Fossil archaeognathan body imprints, *Tonganoxichnus buildexensis,* from Plainville, Massachusetts. (A) Photograph of four specimens, YPM 236969-72, showing variable preservation. (B) Interpretive drawing of (A). Note that the head is preserved in at least three of these examples. (C) Photograph of specimen YPM 227991. (D) Interpretive drawing of (C). (E) Photograph of a specimen on SSM 2011/6-40. (F) Interpretive drawing of (E). Abbreviations as in Fig. 1, with these additions: ab = abdomen; c+tr = coxa and trochanter; h = head; t = tarsus. Scale bars are 5 mm.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c+tr
2
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ab
s
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3
tl
c+tr
t
ab

Figure 5. Body imprints made by the archaeognathan *Trigoniophthalamus alternatus* in wet mud. (A) Jumping trace produced in sediment with a saturation of 46.1%. (B) Interpretive drawing of (A). (C) Jumping trace produced in sediment with a saturation of 46.0%. (D) Interpretive drawing of (C). (E) Jumping trace produced in sediment with a saturation of 40.9%. (F) Interpretive drawing of (E). (G) Landing trace followed by a trackway made as the animal moved to the right in sediment with a saturation of 44.8%. Another segment of the trackway is shown in Figs. 6K-L. (H) Interpretive drawing of (G). (I) Landing trace followed by a jumping trace as the animal stepped sideways and to the left in sediment with a saturation of 46.1%. (J) Interpretive drawing of (I). Abbreviations are as in Figures 1 and 4, except that here the symmetry (left or right) is indicated with the thoracic leg impressions. Scale bars are 2 mm.

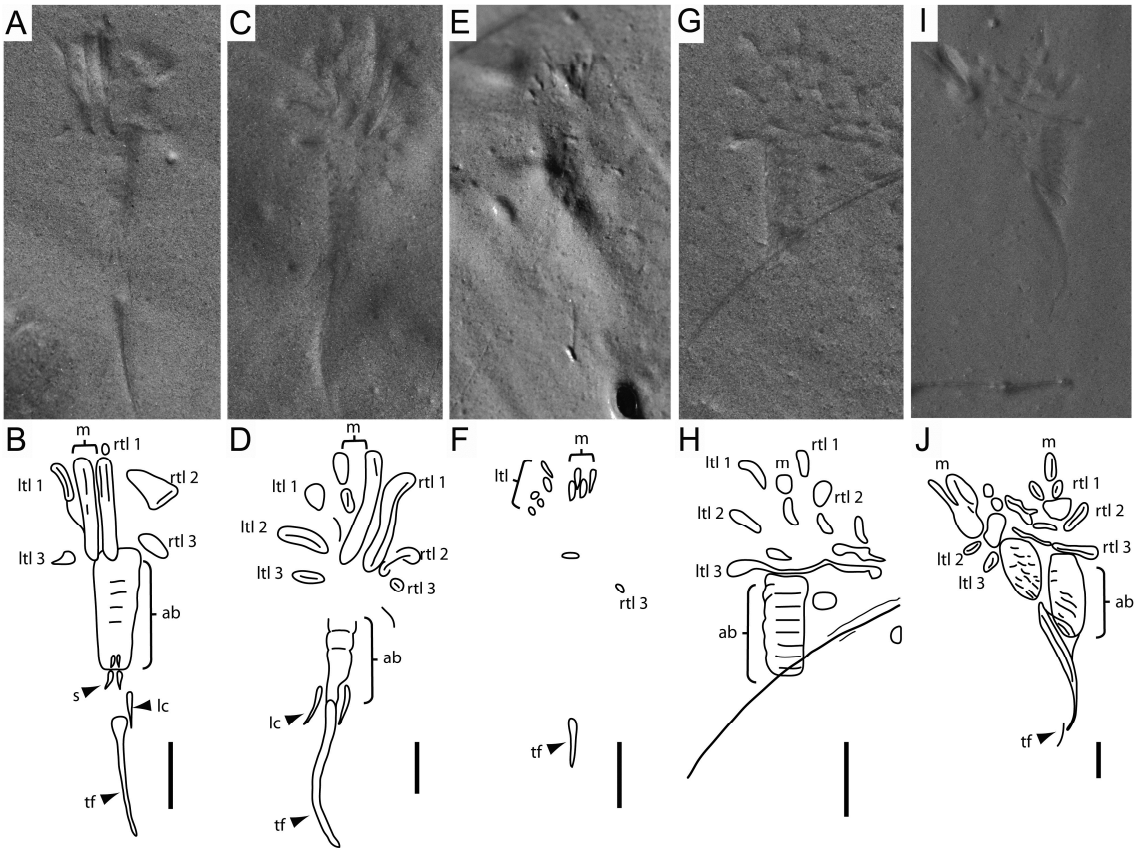
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Figure 6. Experimentally produced archaeognathan trackways. All were produced by *T. alternatus* on wet mud except (I), which was produced by *P. saltator* on smoked glass. Locomotion is from left to right. (A) Walking posture with the terminal filament and/or lateral cerci stuck in the mud. Animals with this posture produced trackways in (B) through (G). (B) Trackway exhibiting a long medial impression produced by the terminal filament and shorter, fainter ones produced by the styli. Saturation is 42.9%. (C) Interpretive drawing of the trackway in (B). (D) Trackway exhibiting a well developed central medial impression produced by the terminal filament, flanked by additional fainter and shorter medial impressions produced by the styli. Note that in the center of the panel there are three medial impressions, as in a fossil from Plainville. Saturation is 45.9%. (E) Interpretive drawing of the trackway in (D). (F) Trackway produced by a bristletail that was struggling in the mud and clawing at the substrate. Saturation is 40.9%. Note the two rows of nearly parallel scratch marks. (G) Interpretive drawing of the trackway in (F). (H) Walking posture with the terminal filament and lateral cerci held off the ground. The styli support the abdomen. Animals with this posture produced trackways in (I) through (N). (I) Trackway exhibiting continuous, closely spaced double medial impressions made by the gonostyli. Note the faint marks left by more anterior abdominal styli lateral to the marks of the gonostyli. (J) Interpretive drawing of (I). (K) Continuation of the trackway in Figs. 5G, here showing two continuous parallel medial impressions produced by anterior abdominal styli, between which are discontinuous “tic marks” produced by the gonostyli. Saturation is 44.8%. (L) Interpretive drawing of (K). (M) Trackway with two rows of medial impressions produced by styli. Saturation is 40.7%. (N) Interpretive drawing of (M). Abbreviations as in Fig. 1 and 4, with this addition: ts= tarsal sets. Scale bars are 5 mm.

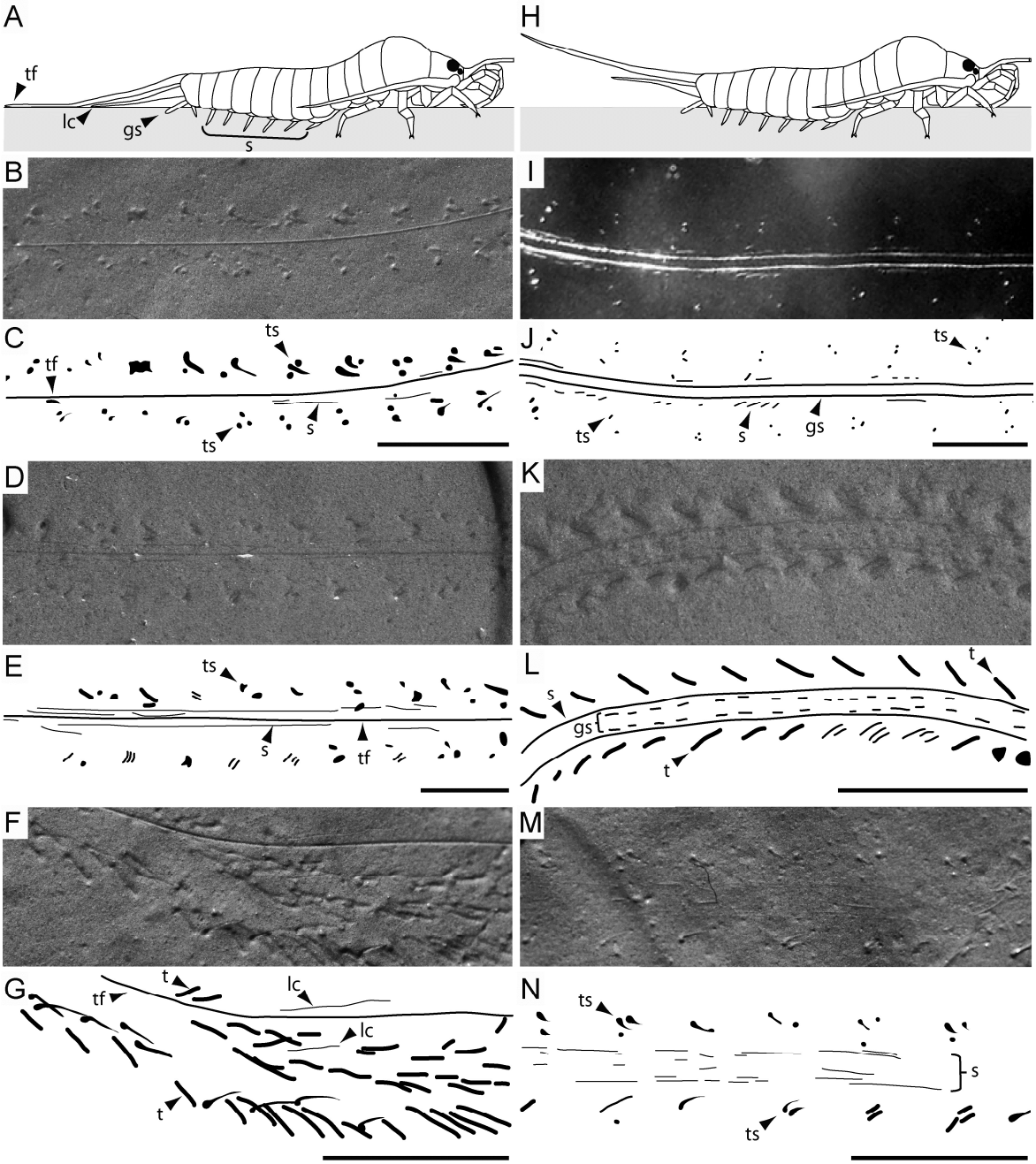
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Figure 7. Experimentally produced thysanuran (*T. domestica*) trackways. The medium is wet mud in all cases except (A), which is smoked glass. Locomotion is from left to right. (A) Trackway exhibiting a long medial impression produced by the terminal filament, which is flanked at irregular intervals by short and faint impressions of the gonostyli. (B) Interpretive sketch of (A). (C) Trackway exhibiting alternating series of tracks, but no medial impression because the terminal filament was held off of the ground. A body imprint is at the left where the animal was dropped into the pan. Saturation is 43.3%. (D) Interpretive sketch of (C). (E) Trackway with discrete tracks arranged loosely into series, and with two long impressions left by the antennae between which are two short impressions left by the terminal filament. Saturation is 42.1%. (F) Interpretive sketch of (E). G) Trackway exhibiting merging tracks with long tapering drag marks and a single medial impression left by the terminal filament. Saturation is 41-43%. (H) Interpretive drawing of (G). (I) Trackway exhibiting a double medial impression produced by the terminal filament and left lateral cercus. Saturation is 41.4%. (J) Interpretive drawing of (I). (K) Trackway made by same individual as in (I), this one with a triple medial impression made by the terminal filament and both lateral cerci. Note that on the left two short impressions were produced by the gonostyli. Saturation is 39-41%. (L) Interpretive drawing of (K), omitting all but the medial impressions for clarity. Abbreviations as in Fig. 1, 4, and 6. Scale bars are 5 mm.

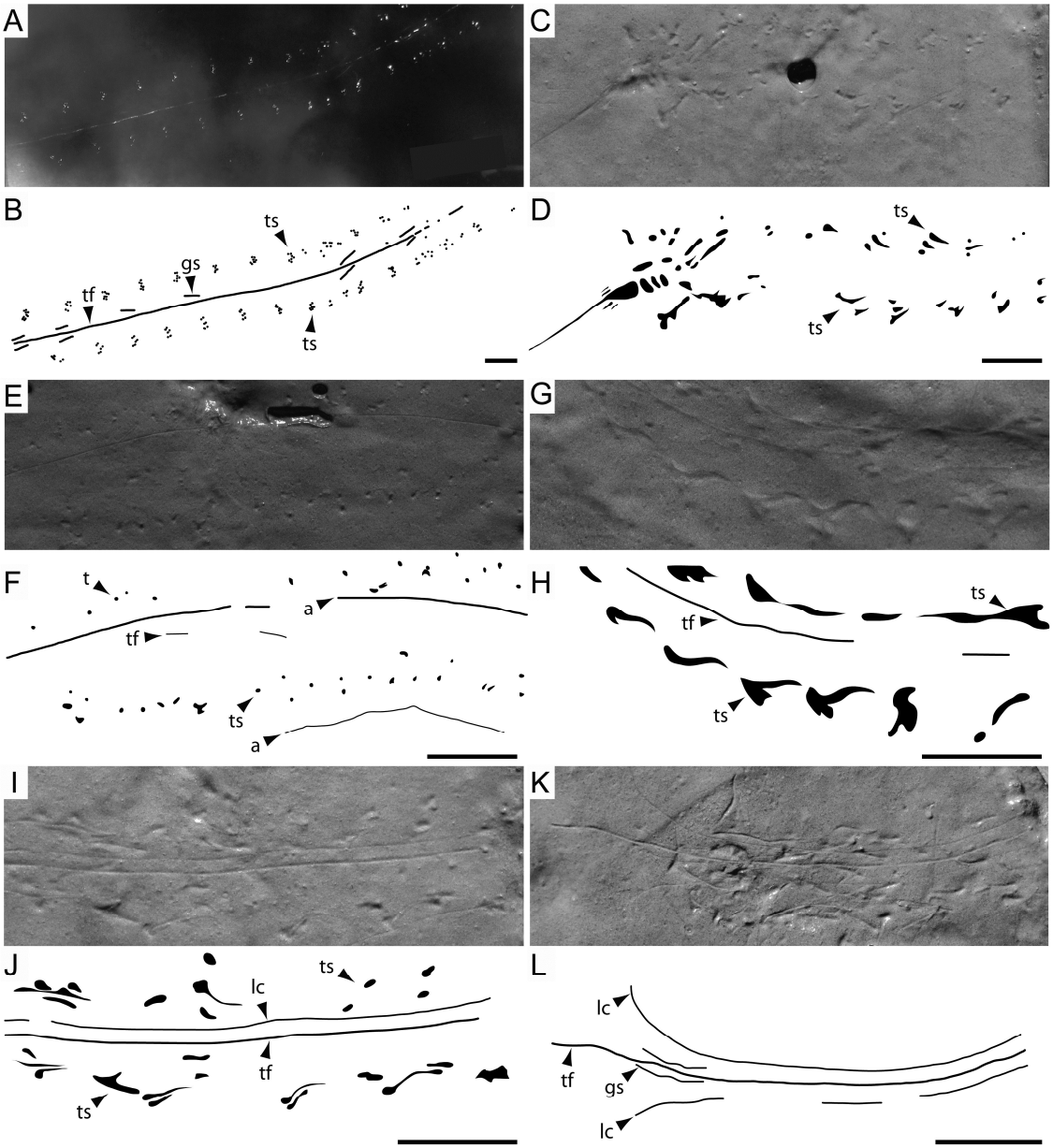
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Figure 8. X-Y scatter plot showing the relationship between sediment desiccation and time. The two shaded regions indicate saturation conditions that were suboptimal for trace production and/or preservation. At high saturation conditions (>45%) loss of detail occurred due to sediment flow, which filled shallow portions of traces, whereas at low saturation conditions (<38-36%) the mud became stiff and resistant to trace production.

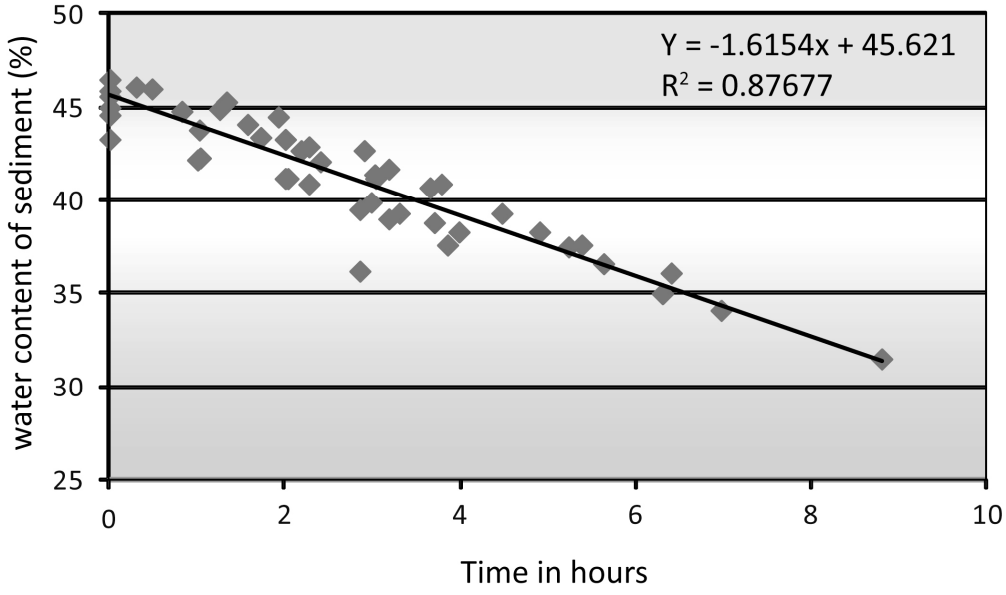
Y = -1.6154x + 45.621
R2 = 0.87677
water content of sediment (%)
50
45
40
35
30
25
0
2
4
6
8
10
Time in hours

Table 1—Occurrences of Archaeognathan body and trace fossils. References: 1= Labandiera et al. (1988), 2= Shear et al. (1984), 3= Brongniart (1885), 4= Rasnitsyn (1999), 5= Engel (2009), 6= Rasnitsyn et al. (2004), 7= Rowland (1997), 8= Duren (1978), 9= Sharov (1957), 10= Belchy and Stockar (2011), 11= Sharov (1948), 12= Sturm and Poinar (1998), 13= Alonso et al. (2000), 14= Grimaldi et al. (2002), 15= Grimaldi et al. (2000), 16= Silvestri (1912), 17= Koch and Berendt (1854), 18= Menge (1854), 19= Olfers (1907); 20= Wygodzinsky (1971); 21= Sturm and Poinar (1997), 22= Mángano et al. (1997), 23= Buatois et al (1998), 24= Mángano et al. (2001), 25= Benner et al. (2011), 26= Getty et al. (2009), 27= Braddy and Briggs (2002), 28= Minter and Mraddy (2006), 29= Minter and Braddy (2009), 30= Lucas et al. (2005a), 31= Lucas et al (2005b).

Taxon	Age	Location	Reference
Body fossils			
Unnamed	Early Devonian	Canada	1
Unnamed	Middle Devonian Late	New York, USA	2
Dasyleptus lucasi	Carboniferous Late	France	3
Dasyleptus noli	Carboniferous	Allier, France	4
Dasyleptus artinskianus	Early Permian	Kansas, USA	5
Dasyleptus rowlandi	Early Permian	New Mexico, USA	6
Dasyleptus sp.	Early Permian	Czechoslovakia	5
Dasyleptus sp.	Early Permian	New Mexico, USA	7
Dasyleptus sharovi	Early Permian	Kansas, USA	8
Dasyleptus brongniarti	Late Permian	Russia	9
Dasyleptus triassicus	Middle Triassic	Switzerland	10
Triassomachilis uralensis	Late Triassic	Urals, Russia	11
Cretaceomachilis libanensis	Early Cretaceous	Lebanon	12
Unnamed	Early Cretaceous	Spain	13
Unnamed	Late Cretaceous	Burma	14
Unnamed	Late Cretaceous	New Jersey, USA	15
Machilis (?) *caestifera*	Eocene	Baltic region	16
Machilis acuminata	Eocene	Baltic region	17
Machilis albomaculata	Eocene	Baltic region	18
Machilis anguea	Eocene	Baltic region	17
Machilis boops	Eocene	Baltic region	19
Machilis capito	Eocene	Baltic region	16, 19
Machilis confinis	Eocene	Baltic region	17
Machilis corusca	Eocene	Baltic region	17
Machilis diastatica	Eocene	Baltic region	19
Machilis electra	Eocene	Baltic region	17
Machilis imbricata	Eocene	Baltic region	17
Machilis longipalpa	Eocene	Baltic region	17
Machilis macrura	Eocene	Baltic region	18
Machilis palaeomon	Eocene	Baltic region	16, 19
Machilis saliens	Eocene	Baltic region	18
Machilis seticornis	Eocene	Baltic region	17
Praemachilis cineracea	Eocene	Baltic region	16, 19
Neomachilellus sp.	Oligocene-Miocene	Mexico	20
Neomachilellus dominicanus	Miocene	Dominican Republic	21
Trace fossils			
Tonganoxichnus buildexensis	Late Carboniferous	Kansas, USA	22
Tonganoxichnus ottawensis	Late Carboniferous	Kansas, USA	22
Stiallia pilosa	Carboniferous	Kansas, USA	23
Stiaria intermedia	Late	Kansas, USA	23

	Carboniferous Late		
Tonganoxichnus buildexensis	Carboniferous Late	Indiana, USA	24
Tonganoxichnus	Carboniferous	Massachusetts, USA	25
Tonganoxichnus buildexensis	Carboniferous Late	Massachusetts, USA	26, this study
Stiaria intermedia	Carboniferous Late	Massachusetts, USA	26, this study
Siskemia elegans	Carboniferous Late	Massachusetts, USA	This study
Stiallia pilosa	Carboniferous	Massachusetts, USA	This study
Tonganoxichnus robledoensis	Early Permian	New Mexico, USA	27, 28, 29
Tonganoxichnus apacheensis	Early Permian	New Mexico, USA	27, 29
Stiaria intermedia	Early Permian	New Mexico, USA	28, 29
cf. *T. robledoensis*	Early Permian	New Mexico, USA	30
Stiaria sp.	Early Permian	New Mexico, USA	30
cf. *T. robledoensis*	Early Permian	New Mexico, USA	31
Stiaria intermedia	Early Permian	New Mexico, USA	31

A new reconstruction of continental *Treptichnus* based on exceptionally preserved material from the Jurassic of Massachusetts

ABSTRACT

The three-dimensional reconstruction of the well-known ichnogenus *Treptichnus* is reassessed based on a large collection of well-preserved burrows from the Lower Jurassic of Massachusetts and the type material from the Mississippian of Indiana. The Jurassic burrows vary greatly in morphology and demonstrate that the stratonomic reconstruction that explains the presence or absence of projections does not work for all *Treptichnus* burrows. Rather, the presence or absence of projections results from minor behavioral changes in the trace maker. Other features of the burrows, such as expanded bulbous projection ends are also shown to result from trace maker behavior. The large sample size and intergradation of specimens also allows the synonymization of *Haplotichnus* and *Plangtichnus* with *Treptichnus*. Finally, a new species is established for morphologically distinct specimens from Massachusetts.

1. Introduction

Treptichnus was established based on continental trace fossils from the Carboniferous of Indiana (Miller, 1889). In plan view the type species, *T. bifurcus*, consists of a series of zigzagging, interconnected segments that bear projections at the segment junctions, giving it a distinctive morphology that is often likened to a sewer's featherstitch (Fig. 1.1–1.2). Because the specimens he collected were preserved in concave epirelief, Miller (1889) considered *Treptichnus* to be a two-dimensional surface trail produced by insect larvae. Miller (1889) also described the ichnogenera *Haplotichnus* and *Plangtichnus* (Figs. 1.3–1.4), which were similar

to *Treptichnus* in exhibiting zigzagging courses, but were differentiated based on their size and lack of projections.

Archer and Maples (1984) and Maples and Archer (1987) reexamined the holotypes of *Treptichnus* along with material from other localities (e.g., Fig. 1.5–1.6). They noted that *Treptichnus* was in fact a subsurface burrow rather than a surface trail. Following Seilacher and Hemleben's (1966, fig. 4c) reconstruction of a Devonian "feather-stitch trail," Archer and Maples (1984) proposed a three-dimensional reconstruction in which *Treptichnus* was composed of a series of conjoined J- or U-shaped segments whose distal ends arced up to the sediment surface (Fig. 1.7). They also argued that the burrows exhibited different morphologies depending on the horizontal plane of exposure (Fig. 1.7a–c). In particular, middle sections through the burrow were suggested to yield the typical *T. bifurcus* morphology with projections (Fig. 1.7b), whereas bottom sections of the burrow yielded traces without projections (Fig. 1.7c). This reconstruction has gained widespread acceptance (e.g., Metz, 1992, 1996, 2007; Buatios and Mángano, 1993a; Buatois et al., 1998; Uchman et al., 1998; Jensen et al, 2000; Rindsberg and Kopaska-Merkel, 2005; Carbone and Narbonne, 2014) and implies that *Plangtichnus* is a junior synonym of *Treptichnus* (Buatios and Mángano, 1993a).

In this paper, we describe a subset of *Treptichnus* from an exceptional assemblage of thousands of well-preserved burrows from Early Jurassic continental deposits of Massachusetts. The large sample size and exceptional preservation of the burrows permit a detailed evaluation of their three-dimensional structure and a test of Archer and Maples's (1984) stratonomic model of morphological variation. Indeed, examination of burrows in plan view and cross-section suggests that much variation attributed to preservation instead reflects trace-maker behavior. Based on our observations of the Jurassic material and the type

specimens, we propose a new morphologic reconstruction of *Treptichnus* from continental settings. We also evaluate the taxonomy of *Treptichnus* and related genera and propose two new species.

2. Geological and Paleontological Context

The Massachusetts *Treptichnus* were collected from a small outcrop on a residential lot in Holyoke, Massachusetts known as the Gary Gaulin track site (42°11’51.74”N, 72°38’41.16”W, Fig. 2). This outcrop exposes approximately 2 m of mudstone and fine-grained sandstone of the Early Jurassic East Berlin Formation, which is part of the Late Triassic through Early Jurassic Newark Supergroup in the Hartford Basin (Cornet et al., 1973). Along with basaltic lava flows, sedimentary strata filled a half graben that formed as Pangea pulled apart during the opening of the Atlantic Ocean (Olsen, 1997). The East Berlin Formation is 145–450 m thick (Hubert et al., 1976) and consists of red mudstones and sandstones deposited in playa lakes as well as gray to black shales produced in perennial, oligomictic, alkaline lakes (Hubert et al., 1976, 1992). The cyclic alternation from playa to perennial lake deposition resulted from climactic changes influenced by Milankovich Cycles (Olsen, 1986).

At the Gaulin site, burrows are preserved on one or two beds near the base of the section. The burrows occur within thin mud drapes between muddy, fine-grained, cross-laminated sandstone beds that are up to 3 cm thick (Fig. 3.1). Sedimentary structures on these beds include oscillation ripple marks and mud cracks, indicating deposition in shallow water followed by drying. Similar beds elsewhere in the East Berlin Formation are interpreted as ephemeral lake deposits (e.g., Drzewiecki and Zuidema, 2007), and we infer the same origin for the *Treptichnus*-bearing beds at this site. The burrows are preserved in full relief, and the

mud drapes in which they occur sometimes spall away from the overlying and underlying sandstone layers such that both the top and bottom of a burrow is visible (Figs. 3.2–3.3). More often, however, the mud drapes adhere to the overlying layer to produce concave epireliefs and convex hyporeliefs, or to the underlying layer to produce convex epireliefs and concave hyporeliefs. Some of these burrows are preserved well enough to reveal two parallel rows of raised structures on opposite sides of the bottom of the burrow (Fig. 3.4), which we infer to have been made by structures (legs?) on the ventral side of the animal. The burrows are distributed patchily and the localized disruption of bedding fabric ranges from 1 to 4 on the scale proposed by Miller and Smail (1997).

Treptichnus is associated with abundant vertical *Skolithos* isp., which are common in the East Berlin Formation as a whole (Gierlowski-Kordewch, 1991; Getty, 2005), as well as occasional horizontal trails resembling *Cochlichnus anguinus* and *Helminthoidichnites tenuis*. Dalman and Weems (2013) reported an arthropod trackway and body imprint from the site that they attributed to a whip scorpion. These fossils are thus the only whip scorpion trace fossils known (Hembree, 2013, p. 156). The dinosaur tracks *Anchisauripus* isp. and *Anomoepus lacertoideus* also co-occur with *Treptichnus* (Dalman and Weems, 2013), indicating the presence of theropods and basal ornithischians at the site (Olsen et al., 1998; Olsen and Rainforth, 2003).

Above the *Treptichnus*-bearing layers, the strata exhibit multiple generations of mud cracks that are irregularly sinuous in both cross-sectional and plan view and that were likely produced in pedogenically altered playa mudflats (Demicco and Gierlowski-Kordesch, 1986; Gierlowski-Kordesch and Rust, 1994). These beds exhibit abundant *Skolithos* isp., occasional horizontal *Planolites* isp. that crosscut ripple marks, medium-sized theropod tracks assigned to

Anchisauripus isp., and a large theropod trackway assigned to *Eubrontes giganteus*. These traces are poorly preserved, in contrast to the excellent preservation on the shallow lacustrine deposits that contain *Treptichnus*.

The type material of *Treptichnus*, *Plangtichnus*, and *Haplotichnus* were originally considered to have come from the Mississippian Kaskasgia Group, and the beds in which the traces were preserved were interpreted as representing the shore of a muddy marine bay (Miller, 1889). However, Archer and Maples (1984) indicated that the fossils were actually from the Pennsylvanian-aged Mansfield Formation and suggested that they were preserved in a freshwater deltaic setting. More recently, Kvale et al. (1989) argued that the Mansfield Formation represents a tidally influenced environment. Archer and Maples (1984) provided a detailed summary of the trace fossils found in association with the Indiana burrows.

3. Materials and Methods

The Jurassic burrows were uncovered in 2000 while the owner was excavating dinosaur tracks on his property (Dalman and Weems, 2013). *Treptichnus*-bearing slabs were removed from approximately 32 m^2 of the southern part of the site, adjacent to the road. The excavation process resulted in the loss of some stratigraphic control, but all burrows came from a few beds about 3-5 cm above the dinosaur footprint-bearing slabs described by Dalman and Weems (2013). The slabs described herein are housed at the Springfield Science Museum in Springfield, Massachusetts, and bear numbers with the institutional abbreviation SSM.

Dimensions such as segment length, projection length, and angle between segments were recorded for 92 well-preserved *Treptichnus* burrows from Holyoke following Archer and Maples (1984, fig. 3.2). Due to the small size of the burrows, the measurements were recorded

from digital photographs using ImageJ software. Fifteen cross sections were produced from nine burrows in order to observe their three-dimensional morphology. The sections were cut either parallel or perpendicular to the burrow segment using a tile saw and then polished.

We also examined the type material of *T. bifurcus*, *P. erraticus*, and *H. indianensis* from the Field Museum in Chicago and topotype material of *T. bifurcus* and *P. erraticus* from the Indiana University Paleontology Collection. The type material of *T. bifurcus* includes two syntypes on a slab labeled UC 54099, and the type series of *P. erraticus* also includes two specimens on slab UC 36077. *H. indianensis* was established with a single type specimen on a slab labeled UC 36076. The topotype material examined included ten slabs labeled 16063-2, one slab labeled 16068-1, and a single unlabeled slab.

4. Observations

4.1 Morphological variability

The Jurassic burrows vary considerably in morphology (Fig. 4–7). Isolated burrow segments scattered about the bedding surface (Fig. 4.1) cannot be assigned definitively to an ichnotaxon. In some cases, however, the unconnected burrow segments are closely aligned, suggesting that the same animal made them (Fig. 4.2). Some of these unconnected, aligned burrow segments grade into *Treptichnus bifurcus*, as is seen in Fig. 4.3, where the burrow begins as a looping series of unconnected segments on the right side of the image and then transitions to *T. bifurcus* on the left.

The *T. bifurcus* morphology is itself highly variable. In some burrows, individual segments are long and thin, the projections are short and approximately the same width as the rest of the segment, and the angle between successive segments is relatively high (e.g., Fig.

3.1). By contrast, other *T. bifurcus* have relatively short burrow segments that diverge at low angles and show long, often bulbous, projections. In some of these latter specimens, the segments on either side are tightly packed together, giving the burrow a rather congested, bushy appearance (Fig. 4.4, right side of image).

As will be discussed in more detail below, some *Treptichnus* burrows lack projections entirely or exhibit them only intermittently along the burrow path (Figs. 4.5–4.8). Some of these burrows (e.g., Fig. 4.6) resemble what is typically called *Treptichnus pollardi* (Buatois and Mángano, 1993a). Segments in these burrows may be short and relatively thick (Fig. 4.5) or long and thin (Figs. 4.6–4.8). Where present, projections are either the same width as the rest of the segment (Fig. 4.8) or end in expanded, bulbous terminations (Fig. 4.4). A few of these burrows resemble a string of beads when segments are arranged end to end (Fig. 4.5).

Although most burrows, when seen in bedding parallel view, have straight or approximately straight segments, in some burrows the segments are curved (Fig. 4.8). Finally, some burrows are composed of a thick central tunnel from which thinner projections radiate in a dense, fan-like pattern as the burrow turns (e.g., Fig. 4.9–4.10). These last burrows do not fit well into any previously described *Treptichnus* species and are here assigned to a new one.

4.2 Occurrence of projections

Of the 92 Jurassic *Treptichnus* that were examined in detail, 28 (30%) had projections at all segment junctions, 56 (61%) exhibited projections at some junctions but lacked them at others, and eight (9%) lacked projections entirely. Four burrows with intermittent projections are illustrated in Fig. 5, where arrowheads mark segment junctions lacking projections. The short looping burrow in Fig. 5.1, which consists of eight segments, has projections at four of

the seven junctions. The projections range from 18 to 43% of the segment length (average = 31%). Fig. 5.2 illustrates another short burrow consisting of seven segments with six junctions, five of which exhibit projections of different lengths (14–43% of segment length, average = 22%). Fig. 5.3 shows a burrow consisting of five segments with bulbous terminations. The first junction lacks a projection, whereas the other four exhibit projections ranging from 16–47% (average = 35%) of segment length. Finally, Fig. 5.4 shows an eight-segment, seven-junction burrow. Four junctions have projections between 10–31% (average = 20%) of segment length. In this last burrow, the junctions that lack projections exhibit round, bulbous expansions in between segments arranged end to end.

Likewise, projections are not present at all junctions of the type and topotype specimens of *Treptichnus bifurcus* from Indiana (Fig. 1.1–1.5). In *T. bifurcus* syntype 1 (Fig. 1.1), projections occur in 40 of 45 segments (89%), where they range from 17–46% of segment length (average = 28%). The arrowhead on the right side of Fig. 1.1 points to a segment junction lacking a projection. In syntype 2 (Fig. 1.2), projections occur in 39 of 41 segments (95%), where they range from 10–36% of segment length (average = 24%). The topotype shown in Fig. 1.5 is composed of seven segments with six junctions, three of which (ii, iv, and vi) exhibit short, straight projections ranging from 9–20% of segment length.

As Maples and Archer (1987) noted, projections occur within the syntypes of *Plangtichnus erraticus*. They occur in 17 of 41 segments (= 41%) in syntype 1 (Fig. 1.4), and 5 of 11 segments (= 45%) in syntype 2 (not illustrated), and are thus less common than in *T. bifurcus*. The projections in *P. erraticus* are short, ranging from 10–32% of segment length in syntype 1 (average = 20%), and 11–21% in syntype 2 (average = 16%).

The type specimen of *Haplotichnus indianensis* also bears projections (Fig. 1.3). The specimen is composed of 53 segments, 18 (34%) of which exhibit projections ranging from 10–44% (average = 27%) of segment length. The projections occur within the looping portion of the trace, but are lacking where the burrow course is approximately straight. As with the second *T. bifurcus* syntype (Fig. 1.2), the projections are disconnected from the rest of the burrow segment to which they belong and this, along with the smaller size of the burrow, may explain why they were previously unnoticed.

4.3 Bulbous ends of segments

Twenty-eight (30%) of the Jurassic *Treptichnus* had segments that were the same width along their entire length. The remaining 64 burrows (70%) exhibited bulbous ends on at least some of the burrow segments (Fig. 6). Fig. 6.1 illustrates a burrow that has bulbs near the end of the trace (one is arrowed), but lacks them at the ends of segments that were produced earlier. By contrast, burrows in Figs. 6.2–6.6 exhibit bulbs at the end of each segment.

The segments within a burrow may gradually widen along their length to produce the bulbous expansion, or the bulbs may occur as an abrupt widening of the segment near its end. The presence of bulbs does not correlate with the arrangement of the segments within a burrow, as traces with zigzagging, straight, or curved courses have them. Most bulbs have well defined boundaries, although in some burrows the boundaries are indistinct and grade into the surrounding bed.

Bulbs are round or ovate in bedding-plane-parallel view, and are typically about 1.3–1.8 times the width of the remainder of the segment. In rare examples, however, they are over three times segment width, and in one burrow they reach 5.6 times wider than the segments, giving

the burrow the appearance of a bouquet of balloons on a string (Fig. 6.2). In one burrow the walls of the bulbs are rugose (Fig. 6.3), whereas in all others they are smooth. In some examples where the burrow is preserved as a concave epirelief, the bulbs are deeper than the remainder of the burrow segment to which they belong (e.g., Fig. 5.4, see arrow). A burrow preserved on the edge of an exfoliating mud lamina confirms this last observation, since the undertrace preserved in the sandstone below the lamina shows a more strongly defined bulb relative to the rest of the segment (Fig. 6.5, see arrow). In some burrows, new segments were observed to begin beneath the bulb of the previous segment but these later segments are not squashed underneath the bulb, as one would expect if the bulbs resulted from compaction (Fig. 6.4, see arrow).

Among the Indiana material, bulbous projections were observed only in *T. bifurcus* syntype 1 (Fig. 1.1). Only 12 of the 40 (= 30%) projection-bearing segments within the burrow exhibited bulbs. The expansions, which are ovate, teardrop shaped, or triangularly shaped, reach a maximum of 2.9 times segment width, although most are narrower.

4.4 Cross-sectional profiles

Thirteen longitudinal and two transverse cross sections were produced from nine different burrows. Five of the cross sections are illustrated in Fig. 7. The uncut specimens are shown in plan view with dashed lines indicating the positions of the cross sections, which are shown in the panels below.

Longitudinal cross sections show that, like *Treptichnus* from other localities, the ends of the segments exhibit openings that communicate with the sediment surface (e.g., Figs. 7.3, 7.5, 7.7 and 7.9). The segments themselves, however, do not always show the U- or J-shape for

which *T. bifurcus* is generally known. For instance, the burrow segment illustrated in Fig. 7.2 is nearly flat along its length, with the opening at its end no higher than the remainder of the burrow roof. At the bulbous end of the segment (left side), the burrow floor dips downward into the underlying sandstone layer. The segment in Fig. 7.3, which is from the same burrow, is also flat along most of its length with a slight downward deflection of the burrow floor at the bulb (left side). It is different from the previous segment in that it takes a very slight upward turn at its end. Thus, the overall pattern of this burrow is horizontal with a slightly sinuous top and bottom.

Two additional burrow segments (Figs. 7.5 and 7.7) also have slightly upturned ends; however, in contrast to previously proposed burrow reconstructions, the segments are slightly concave downward rather than upward. Overall, these segments have a slightly sinuous profile as a result of the concave downward trend of the burrow segments, along with the upturned openings at their end. Of the remaining segments that were sectioned, only one (Fig. 7.9) showed a U-shaped profile, and this burrow was extremely shallow with only slight curvature.

The burrows shown in Fig. 7.1-7.7 are contained within the mud laminae adhering to the bases of the beds, and the overlying cross-bedded sands are separated from the burrows only by these laminae. However, the burrow in Fig. 7.8-7.9 is separated from the main sandstone bed by a mud lamina, a thin layer of sand, and then another mud lamina. The end of the burrow penetrates the thin sand layer (left side). This is the only sectioned specimen that showed the burrow penetrating an overlying sand layer.

5. Discussion

5.1 Presence or absence of projections

Four observations of the Jurassic *Treptichnus* suggest that the presence or absence of projections at segment junctions is not the result of stratonomic sectioning of the burrows, as proposed by Archer and Maples (1984) (see Fig. 1.7). First, the burrows are primarily horizontal in nature and do not have long vertical shafts penetrating thick layers of sediment (Fig. 7). Indeed, where burrows are preserved in full relief (e.g., Fig. 3) the projections show, at most, only minor upturns. Thus, extremely different stratonomic sections are not possible. Second, individual burrows exhibit projections at some junctions but not others (Fig. 5), even when viewed from below on a single plane, such that the presence/absence of projections cannot be attributed to different levels of exposure. Third, when projections are present within a burrow, they are often of different lengths at different junctions, which results from changes in horizontal distance rather than vertical sectioning. Fourth, longitudinal sections (e.g., Fig. 7.2) show that burrow segments are sometimes constructed near or at the end of previous segments, which results in short projections or none at all.

These four observations indicate that the presence or absence of projections in the Jurassic *Treptichnus* results from differences in the placement of new burrow segments relative to the ends of the previous ones. Where projections are present, the animal backed into the older segment before changing direction and excavating a new one. The length of the projection depends on how much the tracemaker backed up; short projections resulted from small retrograde movements whereas long projections resulted from larger retrograde movements. By contrast, burrow junctions that lack projections resulted from the animal constructing new segments directly at the ends of previous ones.

The types of *Haplotichnus*, *Plangtichnus*, and *Treptichnus* are preserved as concave epireliefs on single bedding planes and have intermittent, variable-length projections, which

suggests that their variability also results (at least in part) from changes in horizontal placement of new segments relative to previous ones. The *T. bifurcus* topotype illustrated in Fig. 1.5–1.6, however, more closely matches the stratonomic reconstruction of Archer and Maples (1984; Fig. 1.7) in that the burrow was excavated deeper below the surface, penetrating a 1.8 mm thick lamina to intersect the overlying bedding plane as a series of pits. In bedding-plane-parallel view, projections are intermittently present along the burrow, again suggesting variations in horizontal placement of segments. The projections, however, are all relatively short, and if the lamina preserving the burrow were split, it is likely that the projections would appear longer than they do in the bottom view of the specimen.

Ultimately, it is likely that either or both factors–the horizontal placement of burrow segments relative to preexisting ones and the stratonomic sectioning of the burrow–will affect the presence or absence of projections, depending on the geometry of the specimen at hand. For primarily horizontal burrows, like the Jurassic ones examined here, lateral placement of burrow segments will be the primary controlling factor in the presence of projections, whereas in burrows with more vertically oriented terminal shafts, stratonomic sectioning might play a role as well.

5.2 Origin of the bulbous ends of burrow segments

Jensen (1997) and Wilson et al. (2012) proposed that bulbous projections in marine forms attributed to *Treptichnus pedum* resulted from compaction of vertical shafts. In the Jurassic burrows, segments observed in cross section are often ovate in outline (e.g., Fig. 7), suggesting that the burrows experienced compaction as well. Various lines of evidence, however, indicate that this compaction did not by itself produce the wide, bulbous projections,

although it may have widened the bulbs. For example, some burrows exhibit bulbous, expanded ends on some segments but lack them on others (Fig. 7.1), and burrows exhibiting bulbs also occur next to burrows lacking bulbs entirely (Fig. 7.2). One would expect, however, all of the projections within an individual burrow and all burrows next to each other to exhibit bulbs if these structures were the result of compaction. Finally, in burrows where the successive segments were excavated underneath the bulbous ends of the preexisting segments (e.g., Fig. 6.6, see arrow), the portion of the next segment underneath the bulb is not wider than the rest of the segment, which would be the case if a long, sand-filled tube were being compressed on top of it. These observations suggest that, rather than being the result of compaction, bulbs in the Jurassic material are the result of tracemaker behavior. This hypothesis is further supported by the rugose texture of the bulbs in one burrow, which we infer to be the result of scratching or serial probing during the construction of the bulb (Fig. 6.3), and the greater depth of the bulbs relative to the rest of their associated segments (Fig. 6.4–6.5). As with the Jurassic material, we propose that the slight expansions of the ends of the segments in the type and topotype material from Indiana are also the result of the behavior of the animals that made the burrows.

5.3 Tracemaker identity

The bilateral symmetry exhibited by some of the Jurassic burrows (Fig. 4.2) and the imprints on some burrow floors (Fig. 3.4) suggest an arthropod tracemaker. Modern fly larvae (order Diptera)—including midges (family Chironomidae), horse flies (Tabanidae), and crane flies (Tipulidae) —produce *Treptichnus*-like traces in both naturalistic and lab settings (Seilacher, 1955; Bajard, 1966; Tessier et al., 1995; Uchman, 2005; Martin, 2009). These modern burrows disrupt only the upper few mm of the sediment (Bajard, 1966; Uchman, 2005),

and they can deflect the sediment surface upwards as is seen in shallow horizontal mole burrows. Many of these modern fly burrows are strikingly similar to the Jurassic *Treptichnus*. For example, Uchman (2005, figs. 1–2) illustrated larval midge burrows that resemble fossil burrows illustrated in Figs. 3.6 and 4.4 in having bulbous expansions within the burrow and occasional short projections.

The earliest known definitive dipteran body fossils are mid-Triassic in age (Krzemiński et al., 1994), and diverse dipterans are known from the late Triassic of the Newark Supergroup (Fraser et al., 1996; Blagoderov et al., 2007). Considering that the first occurrence of dipterans predates the Jurassic *Treptichnus*, and that recent fly burrows and their fossil counterparts are remarkably similar, we consider larval dipterans to be the likely tracemakers of the Jurassic *Treptichnus*. However, the type material of *Treptichnus* predates the earliest known dipterans and is attributed to other insects (Miller, 1889).

5.4 Burrow reconstruction

The Archer and Maples (1984) reconstruction of *Treptichnus* does not work well for the Jurassic burrows from Massachusetts because they are primarily horizontal and because the presence or absence of projections reflects tracemaker behavior. In Fig. 8 we provide a new reconstruction for the Jurassic *Treptichnus*. As with modern dipteran burrows, the Jurassic *Treptichnus* are reconstructed as subhorizontal, mole-tunnel-like structures excavated just below the surface, with roofs deflected slightly above their surroundings. Segments were open to the surface, as indicated by the black oval at the end of each. As one follows the top burrow from left to right, the projections get progressively shorter as the new segments are constructed closer to the ends of the preexisting segments. The last segment junction lacks projections due

to the construction of the newer segment at the end of the previous one. The second segment is shown with an expanded, bulbous terminal chamber excavated by the producer, as is the first segment (shown in cross section) in the burrow on the bottom of the figure.

6. Systematic Paleontology

We restrict our current synonymy to continental occurrences of *Treptichnus* and, although we tentatively retain marine species within the ichnogenus, suggest that additional work be done to address concerns raised by researchers such as Rindsberg and Kopaska-Merkel (2005) that these burrows belong to different ichnogenera. Also, we adhere to the ichnoxaxonomic guidelines presented by Bertling et al. (2006) and Minter et al. (2007) for the establishment of new ichnotaxa and the synonymization of preexisting ones. In particular, we consider that synonymy is justified when minor behavioral changes by the trace maker while constructing the trace result in intergrading specimens.

6.1 Ichnogenus Treptichnus Miller, 1889 (Figures 1, 3–7)

1889 *Haplotichnus* MILLER, p. 578, fig. 1086.

1889 *Plangtichnus* MILLER, p. 580, fig. 1093.

1890 *Haplotichnus* LESLEY, p. 1206, fig. 1086.

1890 *Plangtichnus* LESLEY, p. 1206, fig. 1093.

1890 *Treptichnus* LESLEY, p. 1206, fig. 1095.

non 1948 feather-stitch trail WILSON, p. 57, plate 28, figs. 1–3

1966 Feather stitch trail SEILACHER and HEMLEBEN, p. 48, fig. 4c.

1975 *Haplotichnus* HÄNTZSCHEL, p. W67.

1975 *Plangtichnus* HÄNTZSCHEL, p. W95.

1975 *Treptichnus* HÄNTZSCHEL, p. W117, fig. 68.5a–c (in part).

1977 *Haplotichnus* FORNEY et al., p. 28.

1977 *Plangtichnus* FORNEY et al., p. 30.

1977 *Treptichnus* FORNEY et al., p. 32.

1984 *Haplotichnus* ARCHER and MAPLES, p. 450, fig. 4f.

1984 *Plangtichnus* ARCHER and MAPLES, p. 452, figs. 5c, e, g.

1984 *Spirodesmos* ARCHER and MAPLES, p. 455, figs. 5b.

1984 *Trepticynus* ARCHER and MAPLES, p. 455, figs. 5d, f, i, 6 (nom. null.)

1987 *Haplotichnus* MAPLES and ARCHER, p. 890, fig. 2.1.

1987 *Plangtichnus* MAPLES and ARCHER, p. 891, fig. 2.2–3.

1987 *Treptichnus* MAPLES and ARCHER, p. 893, fig. 2.4–5.

1993b *Haplotichnus* BUATOIS and MÁNGANO, p. 242, fig. 3e.

1995 *Haplotichnus* ARCHER et al., p. 2033–4, figs. 6e.

1995 *Plangtichnus* ARCHER et al., p. 2034, figs. 7a–b.

1995 *Treptichnus* ARCHER et al., p. 2035, figs. 7a–b.

2005 *Treptichnus* RINDSBERG and KOPASKA-MERKEL, p. 132, fig. 10 (not *T. apsorum*).

2005 *Haplotichnus* RINDSBERG and KOPASKA-MERKEL, p. 137, fig. 12 (not *H. ornatus*).

6.1.1 Type species

Treptichnus bifurcus

6.1.2 Other species

T. gaulini, T. lubliensis, T. meandrinus, T. pollardi, T. pedum, T. rectangularis, T. triplex

6.1.3 Emended diagnosis

A burrow composed of a series of subhorizontal, J- or U-shaped segments, each of which is open to the surface at its end.

6.1.4 Description

The segments may be connected or disconnected from each other, and together form a straight, zigzag, curved, or irregular system in bedding plane parallel view. Segments can be of uniform width, widen proximally to distally, or be of the same width for most of their length and abruptly expand as bulbous terminations. Where segments are attached, they can originate from the tip of preexisting ones to form straight lines and simple zigzags, or from a point before the tip to form bifurcating projections at the junctions.

6.1.5 Occurrence

The ichnogenus *Treptichnus sensu lato* (see Remarks, below) is widespread, both in temporal and facies distribution. Marine forms assigned to *T. pedum* are a biostratigraphic marker for the Precambrian-Cambrian boundary (Crimes and Anderson, 1985; Narbonne et al., 1987; Brasier et al., 1994), although it and similar traces are now known to occur in the late Ediacaran as well (Jensen et al., 2000; Gehling et al., 2001). Additional marine occurrences are from the Jurassic of France (Schlirf, 2000) and the Eocene of Poland (Uchman et al., 1998).

Continental and brackish water occurrences (*Treptichnus sensu stricto*) are well known from the Carboniferous (e.g., Miller, 1889; Archer and Maples, 1984; Maples and Archer 1987; Buatois and Mángano, 1993a, b; Buatois et al., 1998a, b), the Triassic, (Metz, 1995, 1996, 2000, 2007; Melchor, 2004) Jurassic (Metz, 1992, 1993; this study), and Oligocene (Uchman et al., 2007).

6.1.6 Remarks

Archer and Maples (1984) were the first to suggest that *Plangtichnus* was a morphological variant of *Treptichnus* due to the stratonomic expressions of the latter ichnogenus. Later, Maples and Archer (1987) showed that, like *Treptichnus*, projections also occur in *Plangtichnus*, but they did not propose a formal synonymy between the two. Buatois and Mángano (1993) ultimately did so, although not all subsequent workers have agreed with it (e.g., Archer et al, 1995; Schlirf, 2000). We, however, accept the synonymy for the following reasons: 1) the syntype specimens of *Plangtichnus* exhibit projections at some segment junctions and are therefore transitional with *Treptichnus* (Fig. 1.4), 2) projections are variably present or absent in *T. bifurcus* type material (Fig. 1.1), and 3) transitional forms between the two genera occur among the burrows from Massachusetts (Fig. 5).

Like *Plangtichnus*, we also consider *Haplotichnus* to be synonymous with *Treptichnus* because it exhibits bifurcations and projections at some of its sharply angled turns (Fig. 1.3). The projections are separated from the rest of the burrow segments, and this may be why previous workers (e.g., Miller, 1889; Maples and Archer, 1987; Rindsberg and Kopaska-Merkel, 2005) missed them. Miller (1889), however, noted in his diagnosis of *T. bifurcus* that projections in were sometimes disconnected from the rest of the burrow segment, and thus this

diagnosis encompasses the morphology seen in *Haplotichnus*. Consequently, *Haplotichnus* is better interpreted as a shallow subsurface burrow, like *Treptichnus*, rather than as a surface trail, as has been suggested by some authors (e.g., Buatois and Mángano, 1993b). Furthermore, the presence of projections in *Haplotichnus* preclude synonymization of this genus with *Gordia*, as had been proposed by Buatois et al. (1998).

Since Maples and Archer (1987) revised *Treptichnus* eleven new species have been proposed, mostly for marine forms (Rindsberg and Kopaska-Merkel, 2005, table 2). The validity of many of the species, however, has not been universally accepted (e.g., Buatois and Mángano, 1993a; Rindsberg and Kopaska-Merkel, 2005). In their analysis, Rindsberg and Kopaska-Merkel (2005) were highly restrictive and removed most species from *Treptichnus* based on differences in burrow geometry. *Treptichnus sensu stricto* included only species that were considered shallow subsurface burrow systems inferred to have been made by deposit feeders. Species such as *T. pedum* and related forms were removed to an unnamed ichnogenus because their pattern of bifurcation was considered more irregular, and because burrow segments exhibited blunter terminations. Even more species, considered similar to the ichnogenus *Belorhaphe*, were removed from *Treptichnus* because the zigzagging branches occurred deeper below the surface and thus were inferred to be farming traces.

Our study of the type and topotype *Treptichnus* material indicates that burrows from the type locality are indeed shallow, subhorizontal traces with only a minor vertical component. The Massachusetts material is also shallow and subhorizontal (Fig. 7), and thus fits within the more restrictive definition of *Treptichnus*. We are cautious, however, about removing most marine species from the genus without examining their type material first. We therefore tentatively retain many of the species pending further study.

6.2 Treptichnus bifurcus Miller, 1889

1889 *Haplotichnus indianensis* MILLER, p. 578, fig. 1086.

1889 *Plangtichnus erraticus* MILLER, p. 580, fig. 1093.

1979 *Fustiglyphus roselandensis*, BOYER, p. 75, figs. 2–3.

1990 *Haplotichnus indianensis* BUATOIS and MÁNGANO, p. 78, fig. 2.

1990 *Plangtichnus* sp. BUATOIS and MÁNGANO, p. 80, fig. 2.

1993 *Haplotichnus indianensis* BUATOIS and MÁNGANO, p. 242, fig. 3e.

1993 *Treptichnus pollardi* BUATOIS and MÁNGANO, p. 245, fig. 4d.

1993 *Fustiglyphus roselandensis* METZ, p. 170, fig. 2.

1995 *Treptichnus pollardi* ARCHER et al., p. 2035, figs. 6a–b.

1995 *Treptichnus pollardi* METZ, p. 47, figs. 4d–f.

1995 *Plangtichnus* sp. GREB and ARCHER, p. 101, fig. 9b.

1996 *Treptichnus pollardi* METZ, p. 125, fig. 4g.

1998 Insect trackways ARCHER, p. 24, fig. [1].

non 1998a *Gordia indianensis* BUATOIS et al., p. 155, fig. 4.2.

1998a *Treptichnus pollardi* BUATOIS et al., p. 158, fig. 4.7.

non 1998b *Gordia indianensis* BUATOIS et al., p. 13, fig. 17.

1998b *Treptichnus pollardi* BUATOIS et al., p. 7, fig. 22.

2000 *Treptichnus pollardi* METZ, p. 260, figs. 4a–b.

2004 *Treptichnus pollardi* UCHMAN et al., p. 140, figs. 2b, 5c.

non 2005 *Gordia ornatus* RINDSBERG and KOPASKA-MERKEL, p. 138, fig. 13.

2007 *Treptichnus pollardi* METZ, p. 8, fig. 11.

2007 Insect trail METZ, p. 9, fig. 12.

6.2.1 Emended diagnosis.—Treptichnus composed of a series of conjoined burrow segments with projections variably present or absent at the segment junctions. The burrow has a characteristic zigzag appearance.

6.2.2 Description.—Segments are of variable length along the burrow's length, and may be absent altogether in some places. The angle between burrow segments is also variable and rarely reaches 180°, which produces a straight burrow.

6.2.3 Remarks

The ichnogenus *Plangtichnus* is monospecific, containing only *P. erraticus*. If the synonymy proposed by Buatois and Mángano (1993) is accepted, which we do here, then the question becomes whether or not the species *erraticus* should be retained as separate from *T. bifurcus*. Considering, however, that the ichnospecies *erraticus* exhibits projections at some segment junctions and therefore grades into *Treptichnus bifurcus* at the type locality (Maples and Archer, 1987; Fig. 1.4), we consider the two species as synonyms.

We follow the same logic in arguing that *Haplotichnus indianensis* should be synonymized with *T. bifurcus*. *H. indianensis* exhibits zigzags and has intermittent projections, all of which are characteristics of *T. bifurcus*. Further, if *Haplotichnus* is a junior subjective synonym of *Treptichnus*, the generic assignment of the ichnospecies *H. ornatus* Rindsberg and Kopaska-Merkel (2005) must be reconsidered. Unlike *Treptichnus*, which is a subsurface burrow, the type specimen of *H. ornatus* appears to be a surface trail. Pending reexamination of

the type specimen, we suggest that *H. ornatus* might belong within the ichnogenus *Gordia* or a similar taxon.

Buatois and Mángano (1993) established *Treptichnus pollardi* for traces from the Carboniferous of Argentina that were considered distinct from *T. bifurcus* in lacking projections and in having surficial pits. Additional differences included a more irregular burrow pattern and longer individual segments in *T. pollardi*. Despite the proposed distinction between these two ichnospecies, numerous authors (e.g., Archer et al. 1995; Metz, 1995, 1996, 2007; Uchman et al., 2004) have reported burrows that are transitional between them in having pits at the end of projections along some parts of the trace and having pits directly at the segment junctions in others. Indeed, some of the Holyoke material (e.g., Figs. 4.7, 5.4) also shows transitions between the two ichnospecies. Considering the numerous examples of intergrading specimens, we consider *T. pollardi* to be a junior synonym of *T. bifurcus*.

Finally, Boyer (1979) proposed the ichnospecies *Fustiglyphus roselandensis* for arthropod traces discovered in continental deposits of the Jurassic Brunswick Formation of New Jersey. The fossils consisted of a series of joined segments that have bulbous ends, at which the direction of the trace changed. Metz (1993) also used this taxon for traces from the Boonton Formation of New Jersey. Unfortunately, the holotype was never given to the museum where it was intended to be housed and it is now assumed to be lost (P.S. Boyer, personal comm., 2013). Both traces figured by Boyer (1979) and Metz (1993) superficially resemble *Fustiglyphus*, but Stanley and Pickerill (1993) noted that *Fustiglyphus* has a straight course. The changing course in the New Jersey specimens is consistent with morphological variants of *T. bifurcus* from Massachusetts that zigzag but lack projections due to the placement of successive segments at the end of preexisting ones (Figs. 4.5). We thus propose that *F.*

roselandensis, like *H. indianensis*, *P. erraticus*, and *T. pollardi*, is a junior subjective synonym of *T. bifurcus*.

TREPTICHNUS GAULINI

Diagnosis.—*Treptichnus* consisting of long, thick segments with multiple projections forming a fan-like arrangement at the segment junctions.

Description.—The burrow segments are longer and thicker than those of typical *T. bifurcus* from the same site. Additionally, segmentation is poorly developed in some specimens, where the burrow appears as a long central tube off of which projections emanate. The width of the projections, which sometimes appear pinched off of the rest of the burrow due to sediment compaction, is variable. In the type specimen and one of the paratypes (SSM 2014/X-X) they are narrower than the rest of the segment. In other specimens they are the same width as the segments, expand slightly along their length, or end in abruptly widened bulbs. The fan-like arrays are composed of two to as many as six projections.

Etymology.—This species is named after Gary Gaulin, the owner of the site.

Types.—Holotype SSM 2014/X-X (Fig. 4.10) and paratype SSM 2014/X-X.

Occurrence.—This species is known only from the type locality.

Remarks.—The combination of long, thick burrow segments and the fan-like arrangement of projections distinguishes this taxon from other *Treptichnus* species. This distinctive morphology resulted from the trace maker serially constructing segments offset at slight angles from previous ones, presumably during feeding, before moving forward. In the type specimen, it is not clear why the projections are thinner than the segments, although this may be the result of the segments being an amalgam of multiple thinner segments.

Figure 1. Type and topotype material of *Treptichnus bifurcus* and its junior synonyms from the Pennsylvanian-aged Mansfield Formation of Indiana; specimens are housed at the Field Museum (UC) and the Indiana University Paleontological Collection (IU). (1) close-up of *T. bifurcus* syntype 1 on UC 54099 with an individual segment indicated by a bracket and an expanded, bulbous projection by an arrowhead. (2) Close-up of *T. bifurcus* syntype 2 on UC 54099, which exhibits projections separated from the rest of the segment (3) Close-up of UC 36076, the holotype of *Haplotichnus indianensis*, showing zigzagging and projections separated from the rest of the segment. (4) Close-up of UC 36077 showing *Plangtichnus erraticus* syntype 1, which exhibits projections at the ends of the segments in some portions of the trace. (*5* and *6*) Bed bottom and top views, respectively, of a *T. bifurcus* topotype on IU 16063-2. Ends of segments are labeled in *5* and their corresponding pits on the bed top are numbered the same in *6*. (7) three-dimensional reconstruction of *T. bifurcus* by Archer and Maples (1984) showing proposed changes in burrow morphology resulting from differences in plane of sectioning. Scale bars are 10 mm.

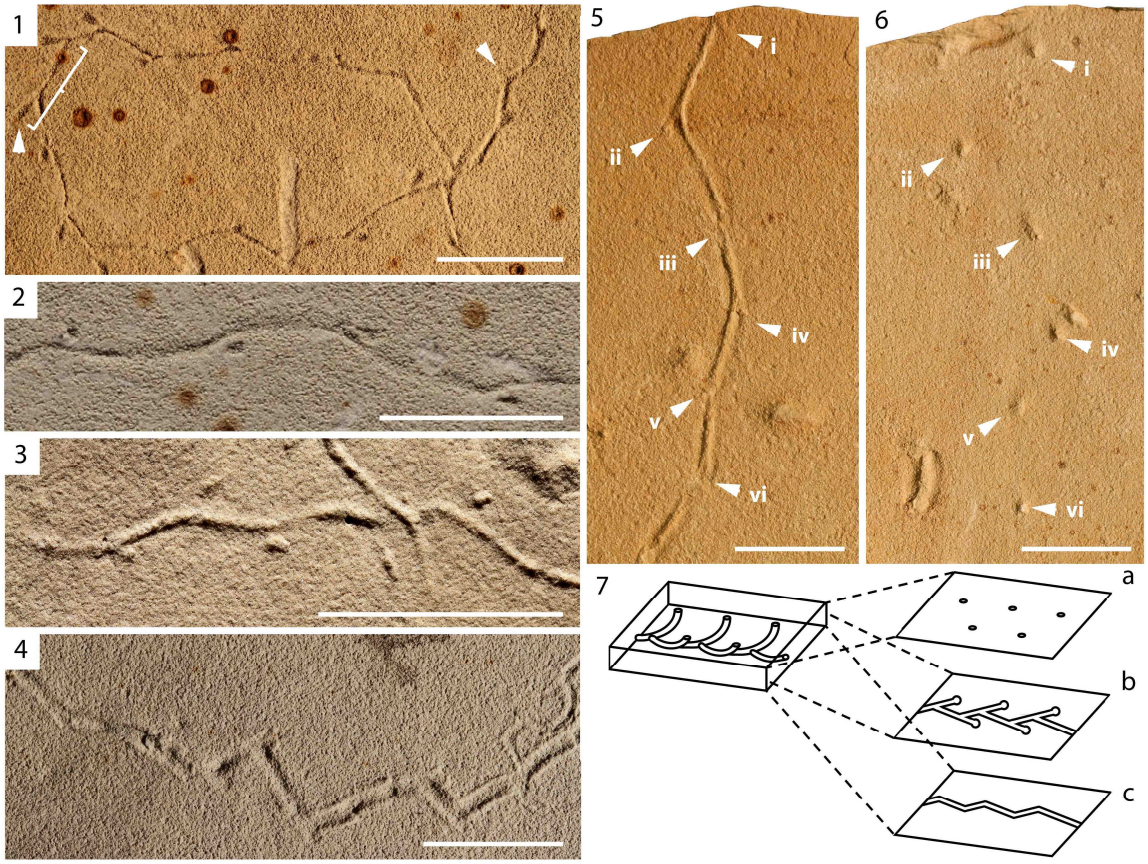
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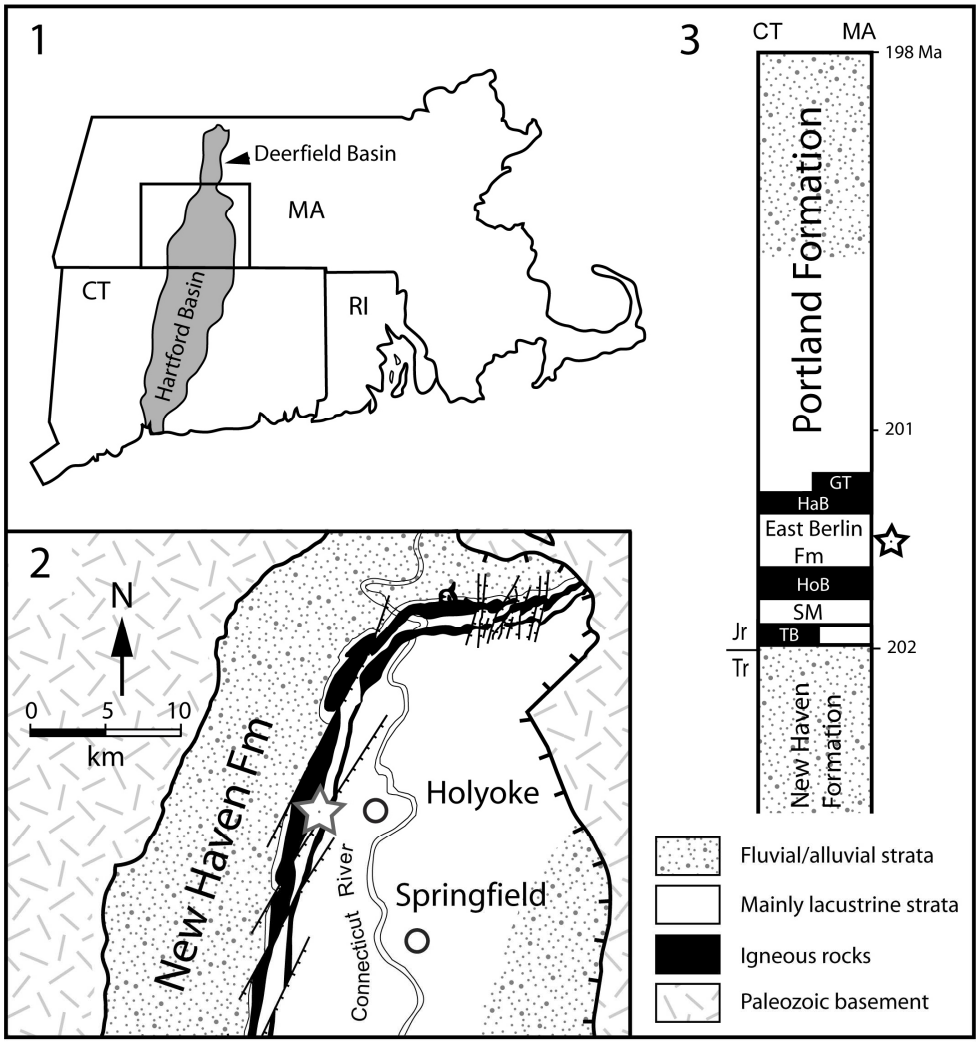
Figure 2. Geography and stratigraphy of the study area. (1) map of southern New England highlighting the distribution of Mesozoic rocks of the Newark Supergroup. (2) Bedrock geologic map of the boxed area in (1). The star indicates the location of the Gary Gaulin dinosaur tracksite, from which the burrows described herein were collected. (3) Stratigraphic column of the Hartford Basin with a star indicating the approximate position of the Gaulin tracksite. (2) and (3) are modified from Collette et al. (2011) and used with permission from Atlantic Geology. Abbreviations are as follows: CT, Connecticut; MA, Massachusetts; RI, Rhode Island; GT, Granby Tuff; HaB, Hampden Basalt; HoB, Holyoke Basalt; SM, Shuttle Meadow Formation; TB, Talcott Basalt.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Portland Formation
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GT
HaB
East Berlin Fm
HoB
SM
Jr
TB
202
Tr
New Haven Formation
Fluvial/alluvial strata
Mainly lacustrine strata
Igneous rocks
Paleozoic basement

Figure 3. *Treptichnus bifurcus* from Holyoke, Massachusetts, showing preservation within thin mud laminae. Specimens are housed at the Springfield Science Museum: *1*, part of 2013/4-03, a bed sole from which the lamina (arrowed) is exfoliating, the dashed outline indicates the position of a flake from the lamina shown in *2* and *3*; *2, 3*, top and bottom views, respectively, of the flake (2013/4-04), showing burrows preserved in full relief; *4*, close-up of the boxed area in *3* showing, between the two brackets, two series of paired ovate imprints preserved on the burrow floor. Scale bars are 10 mm except in *4*, where it is 5 mm.

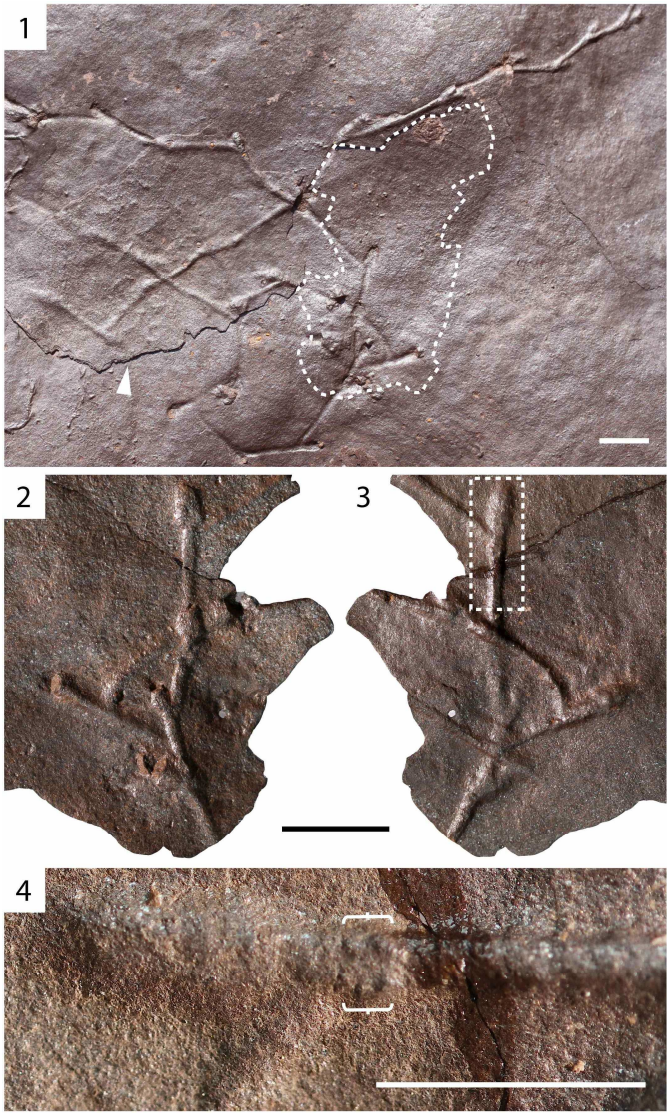
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Figure 4. Morphological variability in burrows from Holyoke, Massachusetts; specimens are housed at the Springfield Science Museum: *1*, SSM 20XX/X-X, showing isolated burrow segments; *2*, SSM 20XX/X-X, showing a burrow composed of aligned, but unjoined segments; *3*, SSM 2014/1-10, showing a burrow starting as unjoined segments that grades into *T. bifurcus*; *4*, SSM 20XX/X-X, a slab on which is preserved a burrow with densely packed burrow segments that have bulbous ends; *5*, SSM 20XX/X-X, a slab exhibiting a burrow with segments aligned end to end and exhibiting bulbous projections; *6*, SSM 20XX/X-X, a slab on which is preserved a burrow with segments arranged end to end but lacking bulbous terminations; *7*, SSM 2014/1-05 a slab on which is preserved a more sinuous burrow with expanded nodes and short projections; *8*, SSM 2013/4-10, a slab on which a burrow with curved segments is preserved; *9*, SSM 20XX/X-X a slab preserving a tightly looping burrow; *10*, SSM 2014/1-08, holotype of the new species *T. gaulini*, showing fanning projections at segment junctions.

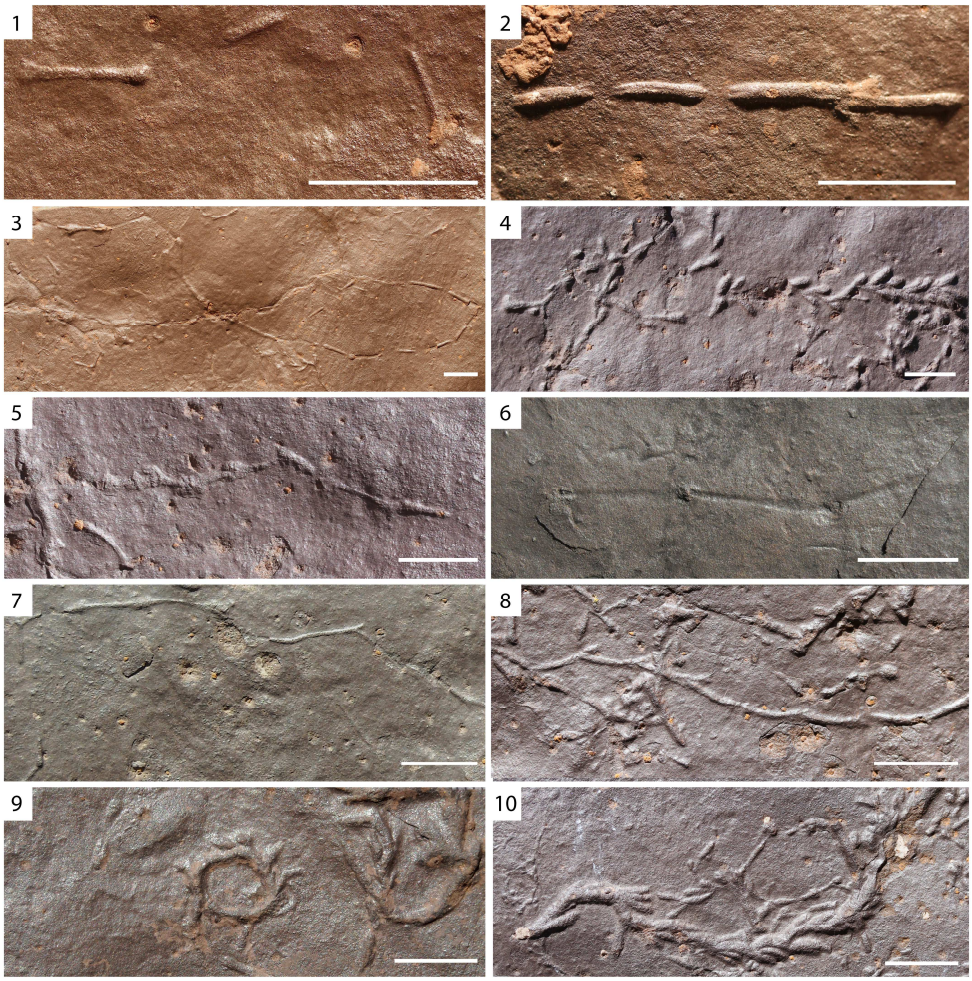
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Figure 5. *Treptichnus bifurcus* showing variation in projection presence and length within individual burrows; specimens are housed at the Springfield Science Museum. (1) Burrow on SSM 2013/4-2 preserved in convex hyporelief. (2) Burrow preserved in concave epirelief on SSM 20XX/X-X. (3) a burrow exhibiting bulbous segment terminations preserved as a convex epirelief on SSM 20XX/X-X. (4) A burrow preserved variably as a concave and convex epirelief on SSM 20XX/X-X. Scale bars are 10 mm.

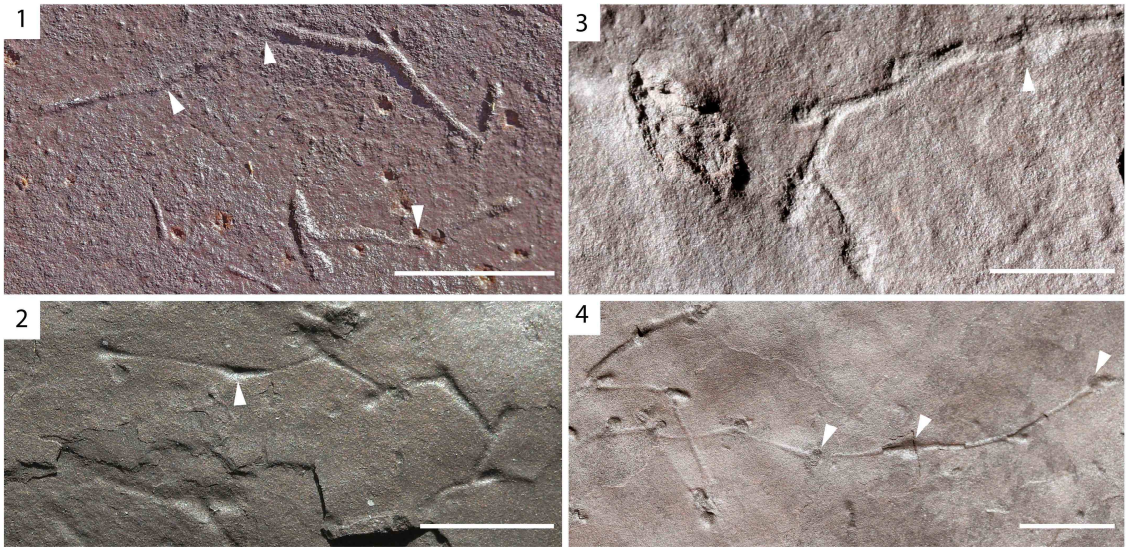
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Figure 6. *Treptichnus bifurcus* with expanded, bulbous distal portions of burrow segments; specimens are housed at the Springfield Science Museum: *1*, part of 2013/4-02, showing a burrow lacking bulbous projections in the segments to the left but exhibiting them in the segments on the right; *2*, burrow on SSM 2013/4-06 preserved as a convex epirelief and exhibiting significantly expanded distal portions of segments (arrowed); *3*, burrow on SSM 2013/4-10 preserved as a convex hyporelief and exhibiting lineations (see arrow) on the bulbs; *4*, a burrow preserved on SSM 2013/4-07 (counterpart is SSM 2014/1-06) as a convex epirelief and exhibiting bulbous terminations that are deeper than the rest of the burrow segments to which they belong; *5*, part of 2013/4-09, a bed top, showing a burrow preserved as a concave epirelief and as an undertrace below the lamina; note that in the undertrace the bulb is deeper than the rest of the burrow segment; *6*, burrow on SSM 20XX/X-X, a bed bottom, preserved as a convex hyporelief and exhibiting an unexpanded proximal portion of a segment below the bulbous distal portion of the preceding segment (arrowed). Scale bars are 10 mm.

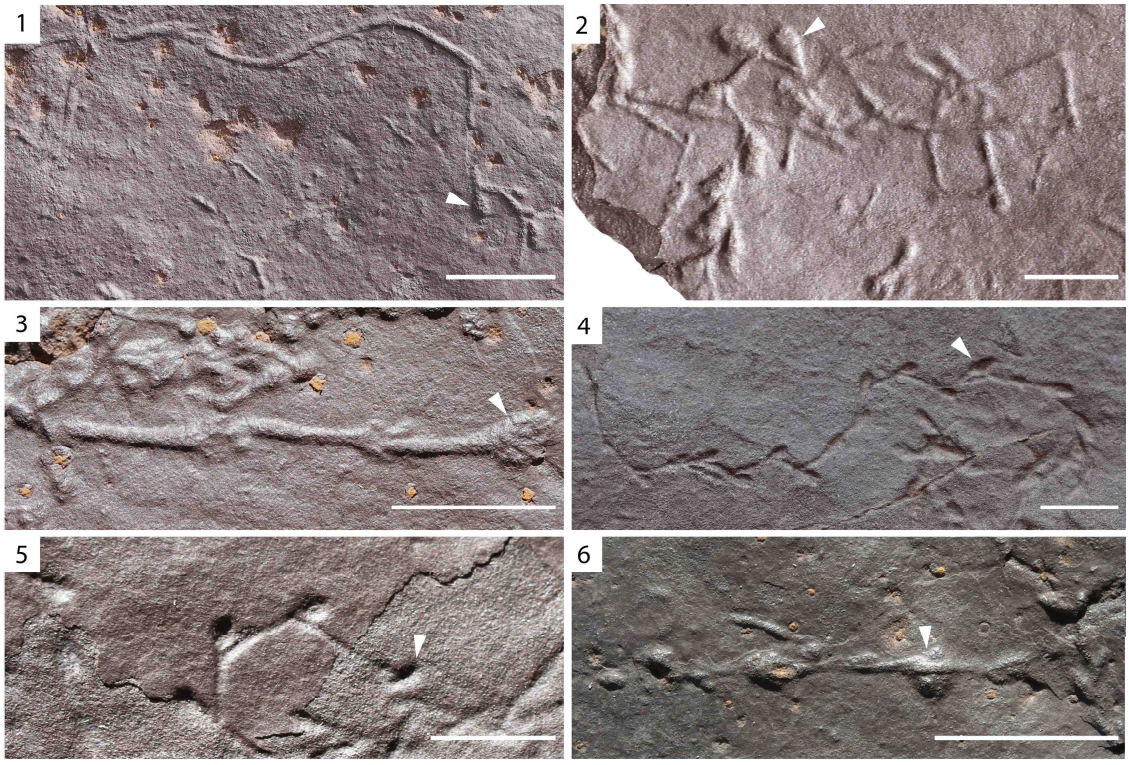
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Figure 7. Longitudinally sectioned *T. bifurcus* from Holyoke, Massachusetts; all are preserved as convex hyporeliefs and are housed at the Springfield Science Museum. (1–3) Overview showing the location of two cuts on 2013/4-12, one on each side of a burrow with expanded projections, and views of the cross sections themselves. Arrowhead in *2* points to the beginning of the following segment, which can be seen as a small ovate structure at the top of the projection. (4–5) Overview showing the location of a cut on 2013/4-13 through a burrow with bulbous projections, and the cross section itself. (6–7) Overview showing the location of a cut along of 2013/4-14 through a burrow with bulbous projections, and the cross section of the segment, respectively. (8–9*)* overview showing the location of a cut through part of 2013/4-11 parallel to a burrow lacking bulbous projections, and the cross section of the segment, respectively. Arrowheads in (9) point to the faint roof of the burrow proximally, and dashed lines distally indicate the position of the roof and floor of the burrow where they become extremely thin. Scale bars are 10 mm in (1), (4), (6), and (8), and 5 mm in (2), (3), (5), (7), and (9).

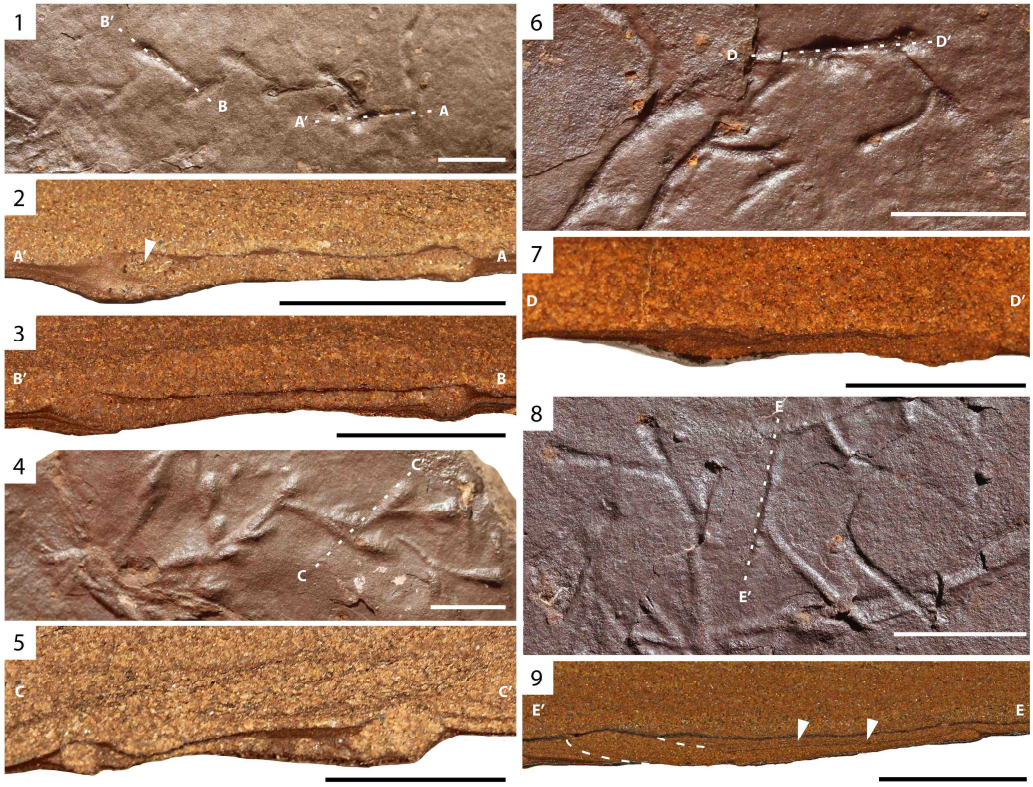
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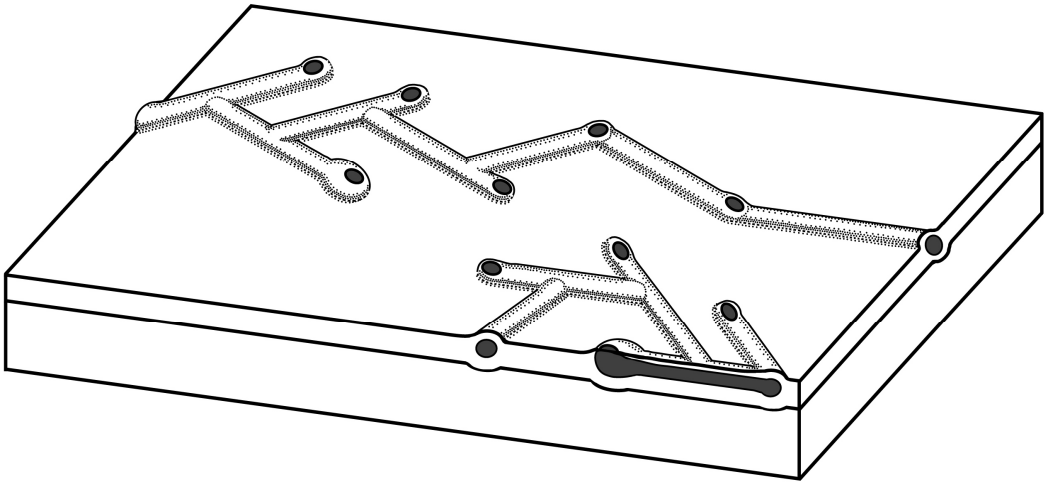
Figure 8. Three-dimensional reconstruction of Jurassic *Treptichnus bifurcus* from Holyoke, Massachusetts emphasizing the burrow's shallowness and the horizontal positioning of subsequent burrow segments relative to the ends of previous ones in determining the presence or absence of projections. The panel shows an oblique view of two burrows as seen at the sediment surface. The gray ovals represent openings to the surface.



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